NOTE TO USERS

The original manuscript received by UMI contains pages with slanted print. Pages were microfilmed as received.

This reproduction is the best copy available

UMI

University of Alberta

OVENBIRDS (*SEIURUS AUROCAPILLUS*) IN RIPARIAN BUFFER STRIPS: SHORT-TERM RESPONSE TO UPLAND TIMBER HARVEST IN ALBERTA'S BOREAL MIXED-WOOD FOREST

by

JAMES DANIEL LAMBERT

©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology & Ecology

Department of Biological Sciences

Edmonton, Alberta
Spring 1998

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisitions et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-28958-3

Canada

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Ovenbirds (*Seiurus aurocapillus*) in Riparian Buffer Strips: Short-term Response to Upland Timber Harvest in Alberta's Boreal Mixed-wood Forest" submitted by James Daniel Lambert in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

Susan Hannon

Dr. S. J. Hannon

Stan Boutin

Dr. S. Boutin

E. Macdonald

Dr. S. E. Macdonald

April 6, 1998

Abstract

In managed forests, riparian buffer strips are maintained primarily to protect water quality. They are also thought to safeguard diverse plant and animal communities. The value of buffer strips to area-dependent and edge-sensitive forest songbirds, however, is largely unknown. Numbers of one such species, the Ovenbird (*Seiurus aurocapillus*), have declined in narrow buffers following upland timber harvest. I assessed the conservation potential of riparian buffer strips for Ovenbirds in Alberta's boreal mixed-wood forest. I measured abundance, territory characteristics, and pairing success in 20m, 100m, and 200m buffers, one year before and one year after upland clearcutting. Following timber harvest, Ovenbirds were absent from 20m buffer strips. Harvesting did not influence abundance, territory size, or pairing success in 100m or 200m buffers. Territories narrowed in both 100m and 200m buffers, though the response was significant only in the latter. Post-harvest territory position did not change in 200m buffers, but territories in 100m strips shifted lakeward, including more habitat adjacent to the riparian edge than before harvest. This positional adjustment may have resulted in changes to the structure of Ovenbird habitat. Further research is necessary to determine whether short-term results reflect long-term effects.

Acknowledgments

This project was supported by the Terrestrial and Riparian Organisms Lakes and Streams study (TROLS), administered by the Department of Biological Sciences at the University of Alberta. TROLS is funded by the Natural Sciences and Engineering Research Council of Canada, Alberta-Pacific Forest Industries, Weyerhaeuser Canada Ltd., Syncrude Canada Ltd., Manning Diversified Forest Products, Ainsworth Lumber Co., C. S. Resources, and Alberta Environmental Protection. This project received additional support from the Canadian Circumpolar Institute and the *Challenge Grants in Biodiversity* Program, Department of Biological Sciences, University of Alberta, and the Alberta Conservation Association.

I am indebted to a host of field technicians whose commitment and professionalism have spurred me to this project's completion. They include: Martha Allen, Brooke Bennett, Sanh Kin Diep, Christine Jamieson, Andrew Jobes, Heather Lowen, Arlette Malcolm, Julie Neville, and Kelly Shortt. Four individuals deserve special recognition for their tireless attention to the wily Ovenbird. They are Brad Smith, Dan Osness, Jacqueline Pollard, and Bonnie Clayton. I hope they consider the product worthy of their efforts.

Ellen Macdonald designed the vegetation sampling protocol. Cindy McCallum and Andrew McAllister provided cheerful and timely assistance from the outset. Their technical support, in countless forms, proved invaluable. I am also grateful for the thoughtful guidance of Claudio Celada, who patiently considered problems of analysis at critical junctures.

My supervisor, Susan Hannon, provided generous financial, logistical, and intellectual support. At the same time, she maintained a challenging and inquisitive lab environment. For her high expectations and the space to work toward them, I am deeply appreciative.

Finally, I acknowledge my wife, Kathy Fallon Lambert, who has been compass, vessel, and harbor on my voyage across two years and too many miles.

Table of Contents

CHAPTER ONE

Riparian Forests, Buffer Strips, and Ovenbirds: A Review

1.1 Introduction 1
1.2 Distinctive Ecological Properties of Riparian Forests 2
1.3 Riparian Forests and Wildlife Habitat 3
1.3.1 Invertebrates 4
1.3.2 Aquatic and Semi-aquatic Vertebrates 4
1.3.3 Terrestrial Vertebrates 5
1.4 Birds in Riparian Buffer Strips 6
1.5 Ovenbirds in Riparian Buffer Strips 8
1.6 Ovenbird Association with Upland Habitat 10
1.7 Ovenbirds and Agricultural Edges 10
1.7.1 Abundance 11
1.7.2 Pairing Success 11
1.7.3 Productivity 12
1.7.4 Survival 13
1.8 Population Status 13
1.9 Ovenbirds in Forested Landscapes 14
1.9.1 Abundance and Pairing Success 15
1.9.2 Predation 17
1.10 A New Methodological Approach 17
1.10.1 The Significance of Territories 18
1.11 Conclusion 20
1.12 Literature Cited 22

CHAPTER TWO

Ovenbirds in Riparian Buffer Strips: Short-term Response to Upland Timber Harvest in Alberta's Boreal Mixed-wood Forest

2.1 Introduction 31
2.2 Methods 34
2.2.1 Description of Forest Type 34
2.2.2 Site Locations 35

2.2.3 Estimating Abundance 38
2.2.4 Territory-mapping 39
2.2.5 Vegetation Analysis 42
2.2.6 Determining Pairing Success 42
2.2.7 Data Analysis 43
2.3 Results 45
2.3.1 Ovenbird Distribution Next to Lakes and Clearcuts 45
2.3.2 Ovenbird Abundance in Buffer Strips 47
2.3.3 Territory Dimensions 50
2.3.4 Territory Position 50
2.3.5 Vegetation Structure 54
2.3.6 Pairing Success 57
2.4 Discussion 58
2.4.1 Ovenbird Distribution Next to Lakes and Clearcuts 58
2.4.2 Ovenbird Abundance in Buffer Strips 60
2.4.3 Territory Dimensions 61
2.4.4 Territory Position 62
2.4.5 Pairing Success 63
2.4.6 Conclusions 64
2.5 Literature Cited 66

CHAPTER THREE

Songbirds in Riparian Buffer Strips of the Boreal Mixed-wood Forest: Analysis of Management Options and Research Needs

3.1 Summary of Findings 71
3.2 Potential Functions of Buffer Strips 72
3.3 Research Needs 75
3.4 Literature Cited 75

APPENDICES

Appendix 1. Delineating Territories with Geographic Information Systems 77
Appendix 2. Nest Predators and Brood Parasites in 100m and 200m Buffers 79
Appendix 3. Ovenbird Nest Sites: Summary and Analysis of Structural Data.....81
Appendix 4. Ovenbird Nesting Data 84
Appendix 5. Ovenbird Territory Maps Before and After Harvest 85
Appendix 6. Distribution of Tennessee Warblers in Interior, Clearcut, and Riparian Sites 101

List of Tables

Table 2.1. Distribution of territory-mapped riparian sites 39
Table 2.2. Mean Ovenbird abundance before and after harvest in 100m and 200m buffer strips and in undisturbed control sites 49
Table 2.3. Effect of upland harvest on Ovenbird territory size and shape 51
Table 2.4. Effect of upland harvest on Ovenbird territory position 52
Table 2.5. Structural characteristics of zone 1 habitat vs. Ovenbird territories.....57
Table 2.6. Percentage of male Ovenbirds paired before harvest, after harvest on the same sites, and after harvest with sites added 58

List of Figures

Figure 2.1. Location of TROLS research areas in Alberta, Canada 36
Figure 2.2. Schematic diagram of a single research area 37
Figure 2.3. Mean number of Ovenbird territories in forests next to lakes, forests next to clearcuts, and in continuous upland forest tracts 46
Figure 2.4. Mean proportion of Ovenbird song perches observed in four designated zones at sites next to lakes and sites next to clearcuts.....48
Figure 2.5. Pre- and post-harvest position of Ovenbird territories in 100m buffers 53
Figure 2.6. Mean proportion of Ovenbird territory area in designated zones within 100m and 200m buffer strips, before and after harvest 55
Figure 2.7. Mean number of Ovenbirds in three riparian forest zones 56

Figure 3.1. Distribution of naturally occurring stand ages and stand ages in harvested areas of an actively managed, silvicultural landscape 74

Chapter One

Riparian Forests, Buffer Strips and Ovenbirds: A Review

1.1 Introduction

In recent years, the Alberta government has leased over 80,000km^2 of the province's boreal mixed-wood forest to pulp and paper companies (Alberta Environmental Protection 1996). This development has raised concerns for the region's wildlife populations. Attention has focused on species whose habitats face alteration and whose numbers have exhibited a negative response to anthropogenic disturbance. The Ovenbird (*Seiurus aurocapillus*) is exemplary in both respects.

In the boreal mixed-wood ecoregion, the Ovenbird is associated with large tracts of mature, poplar-dominated forests (Semenchuk 1992), a vegetation type harvested for the manufacture of pulp and paper. In some areas, virtually all upland poplar stands are scheduled for harvest in a two to three pass cutting regime. Harvest plans call for a minimum of 10 years between passes and a rotation period of 60-70 years. Around lakes larger than 4ha, unharvested reserves are to be maintained in 100m-wide buffer strips, designed primarily to protect water quality (Alberta-Pacific 1993). Recent research suggests that 100m riparian buffers may be too narrow to sustain pre-harvest Ovenbird abundance (Machtans 1996). This thesis evaluates the conservation potential of buffer strips for area-sensitive songbirds, like the Ovenbird. Its purpose is to guide the development of forest management practices that will minimize effects of harvesting on the region's native avifauna.

Objectives of the introductory literature review are four-fold:

(1) to identify distinctive ecological properties of riparian forests;

(2) to survey past avian studies performed in buffer strips;

(3) to synthesize information about Ovenbirds in buffer strips and in other managed environments;

(4) to develop research methods and predictions for an experimental approach.

1.2 Distinctive Ecological Properties of Riparian Forests

Riparian forests occur at the interface between terrestrial and aquatic ecosystems. By virtue of their position in the landscape, they perform unique ecological functions. Consequently, the importance of riparian woodlands is greatly disproportionate to their relative extent (Gregory et al. 1991).

As filters of particulate and dissolved substances (Martin and Pierce 1980, Plamondon et al. 1982, Hornbeck et al. 1986), forests adjacent to lakes and streams govern the form, amount, and timing of sediment and nutrient inputs to receiving waters (Gregory et al. 1991). Immobilization of nutrients in the forest floor and plant biomass conserves watershed nutrient capital while concentrating nutrients in riparian areas (Van Miegroet and Johnson 1993). Elevated levels of nutrients and soil moisture accelerate primary productivity (Johnson et al. 1977, Harris 1984). High plant biomass (Bull 1978) and foliage volume (Swift et al. 1984, Mills et al. 1991) reflect the exceptional fertility of riparian sites.

Riparian plant communities are generally distinguished by high species richness (Gregory et al. 1991, Spackman and Hughes 1995) and species diversity (Bull 1978, Anderson et al. 1980, Gregory et al. 1991, Naiman et al. 1993), arising from sharp resource gradients (Roth 1976, Gregory et al. 1991, Anderson et al. 1980) and dynamic disturbance regimes (Swanson et al. 1988, Gregory et al. 1991). Although fire frequency may be lower in riparian woodlands than in upland forest (Suffling et al. 1982) water-level fluctuations and wind-throws promote the microclimatic heterogeneity that underlies plant species richness and diversity.

Together, disturbance and species diversity help shape forest structure. Thus, riparian areas typically feature higher structural complexity on horizontal (Roth 1976, LaRue et al. 1995) and vertical (Swift et al. 1984, Mills et al. 1991) planes than do upland forests. Because the combination of high primary productivity and high

structural complexity favors high wildlife diversity, riparian areas constitute exceptionally valuable habitat.

1.3 **Riparian Forests and Wildlife Habitat**

Animals are attracted by the abundant food resources and cover that riparian forests provide. In Quebec (Vandal and Huot 1985), Oregon, Wyoming, Arizona, and New Mexico 75%-85% of terrestrial vertebrates utilize riparian areas, some in an obligate association (Chaney et al. 1990). Ohmart et al. (1977) argue that riparian ecosystems surpass all other habitat types in their importance to wildlife. This assertion is supported by generally high measures of animal abundance, richness, diversity, and degree of endemism in riparian ecosystems (Budd et al. 1987).

Climate and topography impose variability on this pattern. Upland-riparian differences are most pronounced in arid landscapes, where scarcity of water sharply restricts the distribution of organisms. In such areas, biological activity is concentrated in stream valleys and topographic depressions. Topography is also an important factor in humid environments, where water is not a severely limiting resource. Topography influences the availability of nutrients and moisture such that landscapes with dramatic relief are expected to have the most pronounced productivity gradients. Conversely, low-relief landscapes, particularly those in forested regions, feature more subtle differences between upland and riparian areas. In the boreal-mixed-wood forest, for example, adjacency to open water does not influence forest age or canopy composition at the scale measured by the Alberta Vegetation Inventory (minimum mapping unit = 0.4ha) (Burgess 1997). However, research performed at a finer scale shows significant, but small differences in nutrient availability, canopy structure and composition (S. E. Macdonald, pers. comm.). Riparian edge effects on subcanopy structure and composition are also difficult to detect, as they penetrate as little as 5m and rarely over 40m into the forest (K. Harper, pers. comm.). Nonetheless, even

subtle habitat distinctions in this low-relief region can result in remarkable effects on wildlife near lakes (Machtans 1996).

The quality of riparian habitat varies with climate and topography. Use of riparian areas by wildlife may also differ between streams and lakes due to geometric distinctions between linear water courses and non-linear water bodies. For example, mammals travelling between two points may be more likely to follow stream channels than lakeshores. Because streams are typically bordered by two structurally diverse and resource-rich ecotones, one on each bank, they may attract more wildlife than a single lakeshore ecotone. However, if a stream is not wide enough to maintain a canopy gap, its adjacent forest may lack the high primary productivity and varied structure that is characteristic of a lake edge exposed to sunlight. Unfortunately, the literature contains no explicit comparison between lake- and stream-side habitat quality. Overall, however, the evidence suggests that plant community's situated at the water's edge are important for invertebrate and vertebrate, aquatic and terrestrial wildlife.

1.3.1 *Invertebrates*

In many regions, deciduous vegetation predominates in riparian forests. The lack of investment by broad-leafed plants in chemical or structural defenses may allow insect herbivores to excel near water (Krueper 1992). Insect abundance in a riparian forest is further enhanced by eggs hatching from the adjacent aquatic system, which derives much of its energy from terrestrial organic matter (Budd et al. 1987). By regulating temperature and inputs, and providing shoreline habitat structure, riparian vegetation influences the abundance, composition, spatial distribution, and production of aquatic invertebrates (review in Gregory et al. 1991). In general, riparian areas produce more insects than upland areas (Jackson and Fisher 1986, Gray 1993).

1.3.2 *Aquatic and Semi-aquatic Vertebrates*

Riparian forests are similarly important to aquatic and semi-aquatic vertebrates, as they regulate water chemistry, moderate water temperature, supply food resources and

provide shoreline structure (Budd et al. 1987). Protecting the terrestrial-aquatic interface reduces effects of upland disturbance, such as sedimentation and eutrophication, on fish populations (Hornbeck et al. 1986). Amphibians may also benefit from conservation of riparian forests since woodlands adjacent to water can harbor unique assemblages of this group (Brode and Bury 1984 as cited by Chapman et al. 1996,). Mammalian predators on fish and amphibians [e.g. otter (*Lutra canadensis*) and mink (*Mustela vison*)] and herbivorous mammals associated with water [e.g. muskrat (*Ondatra zibethica*) and beaver (*Castor canadensis*)] make use of riparian forests for foraging, breeding, and shelter (Castelle et al. 1992).

1.3.3 *Terrestrial Vertebrates*

Terrestrial mammals are also concentrated in riparian settings. Spackman and Hughes (1995) reported that most movement in Vermont forests by white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), fox (*Vulpes vulpes, Urocyon cinereoargenteus*), snowshoe hare (*Lepus americanus*), and vole (*Microtus spp.*) followed the high-water mark of streams. Cross (1985) and Doyle (1990) compared small mammal species richness in riparian vs. upland zones. Both researchers discovered greater species richness in riparian areas, which contained all species captured in the upland.

Birds have received more attention than any other wildlife group in comparisons of uplands with riparian areas. Many studies indicate that forests adjacent to water support greater abundance (Stauffer and Best 1980, Gates and Giffen 1991, Machtans 1996, Stevens et al. 1977, LaRue et al. 1995), species richness (Stauffer and Best 1980, Stevens et al. 1977, Machtans 1996, Gates and Giffen 1991, LaRue et al. 1995) and diversity (Gates and Giffen 1991, LaRue et al. 1995). Emmerich and Vohs (1982) attributed high abundance and species richness in South Dakota riparian woodlands to greater vegetation complexity compared to upland forest tracts. Similar observations by LaRue et al. (1995) in Quebec support the importance of structural

diversity. In situations where the riparian-upland gradient is relatively uniform, differences in bird communities may be slight. Three comparisons between structurally similar riparian and upland forests (Hooper 1991, Small and Hunter 1989, Murray and Stauffer 1995) detected no riparian influence on avian abundance or species richness, though all described one or more species unique to the land-water ecotone.

The works of McGarigal and McComb (1992) and Spackman and Hughes (1995) raise the possibility of a negative riparian effect on birds. In Oregon, forest along upland transects had higher densities, richness, and diversity than riparian counterparts (McGarigal and McComb 1992), while in Vermont most bird species occurred 150m to 175m up-slope from waterways (Spackman and Hughes 1995). The shoreline concentration of predator (Harris 1984, Spackman and Hughes 1995) and brood parasite activity (Gates and Giffen 1991, Machtans 1996) may help explain these unusual patterns.

The suitability of riparian habitat for birds varies among forest systems. Habitat suitability will vary, too, among wildlife species. In a given forest type, understanding specific effects of land-use practices on riparian fauna is required to develop appropriate management standards.

1.4 Birds in Riparian Buffer Strips

Currently, silvicultural practices which conserve lake- and stream-side forests are primarily designed to protect water quality. Retaining strips of riparian forest moderates the export of water, nutrients, soil and woody material to aquatic environments (Martin and Pierce 1980, Plamondon et al. 1982, Hornbeck et al. 1986). In addition, buffer strips provide people with recreational opportunities (e.g. hiking, hunting) and aesthetic services, while safeguarding plant and wildlife habitat. Regrettably, little is known about the effects of upland timber harvest on wildlife in buffer strips. Once again, the ornithological literature provides the most detailed insight.

Birds displaced from altered habitat may crowd into remnant habitat patches shortly after disturbance (Hagan et al. 1996). Darveau et al. (1995) observed this phenomenon in stream-side buffer strips of varying width (20m, 40m, 60m) in boreal balsam fir (*Abies balsamea*) stands of Quebec. In the year after cutting, buffer strip bird densities increased 30%-70% and declined to near pre-treatment levels over the succeeding two years. Machtans (1996) detected less pronounced post-harvest crowding in 100m buffers bordering a lake in Alberta's boreal mixed-wood forest. In contrast, Whitfield and Hall (1997) reported no change in post-harvest bird density in 30m strips adjacent to Ontario wetlands. The observed variation may be explained by inconsistent definitions of buffer width or, more likely, by variable proportions of removed vs. remnant forest cover.

A more consistent finding is the change in bird species composition after treatment, characterized by an influx of species associated with edges and loss of species associated with interior forest. In 20m buffer strips in Quebec, four "ubiquitous" species increased 65% after harvest (Darveau et al. 1995). Three edge-associated species observed in a 1,800m x 80m buffer strip in Maine were absent in an undisturbed reference site (Johnson and Brown 1990). Conversely, the undisturbed lakeshore contained 3 area-sensitive species and 3 cavity nesting species absent in the buffer strip. Several studies (Stauffer and Best 1980, Triquet et al. 1990, Darveau et al. 1995, Machtans 1996) support the pattern of forest interior species loss from buffer strips.

Recent work has focused on the function of riparian buffer strips as movement corridors. In Alberta, lakeshore buffer strips channeled juvenile bird dispersal between forest patches (Machtans et al. 1996). The use of buffer-corridors by songbirds ameliorated effects of disturbance in connected forest patches, which had lower post-harvest turnover than isolated fragments (Schmiegelow et al. 1997). However, Spotted Owl (*Strix occidentalis*) researchers point out the hazards of corridors to birds. They

argue that linear direction of naturally random dispersal patterns (Noss 1992) and high predator concentrations (Thomas et al. 1990) diminish the value of corridors.

Wilcove (1985) found that among forest fragments, riparian buffers featured the highest rate of artificial nest predation (48%) in Maryland. Predator concentrations along forest clearcut edges (Gates and Gysel 1978, Andren 1992) and in riparian habitats (Harris 1984, Spackman and Hughes 1995) may pose a two-sided threat to songbirds in buffer strips. The threat is compounded by the preference for riparian zones exhibited by brood-parasitizing, Brown-headed Cowbirds (*Molothrus ater*) (Gates and Giffen 1991, Machtans 1996).

Whether corridors promote (Henein and Merriam 1990) or diminish (Schmiegelow et al. 1997) the chance of local extinction, the importance of width is certain (Saunders et al. 1991, Chapman et al. 1996). Wide buffer strips will conserve more species (Stauffer and Best 1980, Johnson and Brown 1990, Darveau et al. 1995, Spackman and Hughes 1995) and better facilitate movement of biota (Saunders et al. 1991) than narrow buffer strips. The outstanding challenge, then, is to identify a sufficient width. Ultimately, determination of riparian buffer widths will be influenced by practical constraints and management priorities. In addition, appropriate widths will vary among regions, with differences in ecosystem properties and species of concern.

1.5 **Ovenbirds in Riparian Buffer Strips**

In the ecosystem of interest here, the boreal mixed-wood forest, the Ovenbird (*Seiurus aurocapillus*) is perhaps the best study organism on which to focus population-level research. This neotropical, migratory warbler (1) is associated with mature woodland (Van Horn and Donovan 1994), (2) is abundant in riparian forest stands (Hannon, unpubl. data), (3) is considered both area-sensitive (Galli et al. 1976, Lynch and Wigham 1984, Robbins et al. 1989a, Wenny et al. 1993, Villard et al. 1993, Burke and Nol 1998) and edge-sensitive (MacClintock et al. 1977, Anderson et al. 1977, Kroodsma 1984, Wenny 1989, Burke and Nol 1998), and (4) is easily

monitored due to its conspicuous vocalizations. Though it has received little attention in western boreal forests, the Ovenbird has been the subject of over 60 years of research in eastern and central North America. Some of this work demonstrates that it is sensitive to buffer strip width.

Following clearcutting in Kentucky, Ovenbirds were not retained in narrow (15m-23m) stream-side buffer strips (Triquet et al. 1990). In 100m lakeshore buffers in Alberta, Ovenbirds were also reduced in number during the post-harvest breeding season (Machtans 1996). Researchers in Iowa estimated that a minimum riparian buffer width of 175m was required to support this species (Stauffer and Best 1980). However, Johnson and Brown (1990), working in a 70m-100m buffer, found numbers comparable to an undisturbed, lake-side control.

The applicability of these findings to a management context is limited for four reasons:

1. *Inconsistency.* No definitive pattern emerges from these studies. This is particularly problematic considering the small number of relevant investigations.

2. *Low replication.* Johnson and Brown (1990) and Triquet et al. (1990) surveyed a single buffer strip each, while Machtans (1996) monitored two. Stauffer and Best (1980) did not provide sample size details, but apparently surveyed a single replicate for each of a range of widths.

3. *Sampling methods.* In each case, abundance estimates were derived from periodic point counts or spot-maps of singing males. Unless verified by more intensive observation, these methods may underestimate the number of paired males, which sing about one-third to one-half as often as unpaired males (Lein 1981, Gibbs and Wenny 1993). The difference in detectability casts a shadow of doubt on unconfirmed estimates based on singing male surveys.

4. ***Density is not a reliable indicator of habitat quality.*** Habitat quality may be poor in densely settled patches (Van Horne 1983, Vickery et al. 1992). Density estimates may

be particularly misleading for Ovenbirds in silvicultural landscapes, where males have been observed to crowd in forest fragments, with low probability of mating (Hagan et al. 1996).

A more refined experimental approach will aid in interpretation of existing data sets and reveal patterns that may properly guide buffer strip design. Development of hypotheses and appropriate research methods necessitates a review of Ovenbird response to the two features which most plainly distinguish riparian buffer strips: their location next to water and the predominance of edges.

1.6 **Ovenbird Association with Upland Habitat**

Throughout much of its breeding range, the Ovenbird is more common in upland forest tracts than in riparian areas (in Minnesota - Hawrot and Niemi 1996, Collins et al. 1982; in Missouri - Wenny et al. 1993; in Quebec - LaRue et al. 1995; in Maryland - MacClintock et al. 1977, Robbins et al. 1989a). Research on its Central American wintering grounds suggests resource segregation as a mechanism underlying this pattern. Where Ovenbirds occur with waterthrushes (*Seiurus spp.*), they occupy dry sites up-slope of their congenerics, which utilize moist lowlands (Dickey and van Rossen 1938, Lack and Lack 1972). This pattern is evident in Missouri forests as well, where Wenny et al. (1993) observed habitat segregation among ground-nesting warblers along a local topographic gradient. Ovenbirds were associated with moderately sloped, upland areas, Worm-eating Warblers (*Mellmitheros vermivora*) with steep slopes and Kentucky Warblers (*Oporornis formosus*) and Louisiana Waterhtrushes (*Seiurus motocilla*) with moist depressions in the landscape.

1.7 **Ovenbirds and Agricultural Edges**

The second definitive feature of riparian buffer strips is the predominance of edge, an inherent quality of linear forest tracts. Compared to convex polygonal and circular reserves of equal size, forest strips contain a higher degree of edge per unit area (Diamond 1975). A typical buffer strip is susceptible to edge effects penetrating from

both the clearcut and lake-side openings. However, edge effects must be considered in conjunction with area effects. In heavily fragmented, agricultural landscapes, where the majority of Ovenbird work has been performed, edge and area effects inevitably interact and are not readily distinguishable. Alone or interactively, they influence Ovenbirds in a remarkably consistent fashion. Near edges and in small forest fragments, Ovenbird abundance, pairing success, productivity and survival is low compared to forest interiors and larger patches.

1.7.1 *Abundance*

Studies focused on the relationship between edges and Ovenbird abundance have shown a negative relationship. Higher densities in forest interiors were reported by MacClintock et al. (1977), Wenny (1989), Anderson et al. (1977), and Kroodsma (1984). Comparisons of Ovenbird populations among fragments of different size have shown that fragment size and density are positively correlated (Galli et al. 1976, Robbins et al. 1989a, Gibbs and Faaborg 1990, Wander 1985, Villard et al. 1993, Wenny et al. 1993, Burke and Nol 1998). Edge avoidance may partially explain the results from the latter studies, since smaller habitat patches have a disproportionately low amount of core area (Diamond 1975).

1.7.2 *Pairing Success*

In edge-dominated forests within agricultural mosaics, Ovenbird pairing success is also low. In Missouri, males holding territories <300m from an edge had significantly lower probability of mating than those holding territories >300m from an edge (Van Horn et al. 1995). Likewise, occupants of small fragments paired less frequently than those in large fragments in New Jersey (Wander 1985), Missouri (Gentry 1989, Gibbs and Faaborg 1990), Pennsylvania (Porneluzi et al. 1993), Ontario (Villard et al. 1993, Burke and Nol 1998) and Quebec (Villard et al. 1993). Overall estimates of Ovenbird pairing success in edge-dominated habitats range from 0%-59%, compared to 65%-87% in contiguous forests.

A skewed sex ratio in Ovenbirds, due to higher mortality among females (Hann 1937) largely explains the universal occurrence of bachelor males. Although polygyny has been observed in Ovenbirds (Hann 1937), reports of it are rare. Females that survive the predatory risk and metabolic cost of egg-laying, incubation, and brooding (Gibbs 1988), plus exclusion by males from optimal habitat on the wintering grounds (Rappole and Warner 1980), preferentially breed in extensive forests, away from edges.

1.7.3 *Productivity*

One explanation for Ovenbird selection of interior forest is that habitat near agricultural edges and in forest fragments is less productive for nesting (Porneluzi et al. 1993, Donovan et al. 1995, Burke and Nol 1998, but see Wander 1985). Causes of Ovenbird nest failure vary regionally, but brood parasitism and predation are the most frequently cited. In extreme cases, Brown-headed Cowbirds can parasitize over half of the Ovenbird broods in an area (Hann 1937). Lesser values are typical (see Van Horn and Donovan 1994) in part because, relative to other species, the Ovenbird is a poor host for Cowbirds. In parasitized nests, Ovenbird young grow at nearly normal rates while cowbird fledglings weigh 20% below average (Robinson 1992). Still, Donovan et al. (1995) reported 5.27% and 16.7% daily mortality rates attributable to parasitism in Missouri and Wisconsin/Minnesota fragments respectively. These values exceeded measures of 2.25% and 5% in contiguous forests.

Ovenbirds fall prey to the suite of predators which typify North American agricultural landscapes, including Blue Jays (*Cyanocitta cristata*), gray squirrels (*Sciurus carolinensis*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) (Van Horn and Donovan 1994). Like those of other forest songbirds breeding near edges (Gates and Gysel 1978, Wilcove 1985), Ovenbird nests in fragments experience high (5%-8%) daily predation rates (Robinson 1992, Robinson et al. 1995). Although eggs and nestlings are assumed to be most commonly depredated,

incubating females are also vulnerable. This is due to their tendency to remain on the eggs at the approach of a predator until the final moment, when they flutter away on the ground, feigning injury (Hann 1937, Lein 1980, pers. obs.). Females will spend up to a month on the ground in nesting activities (Bent 1953), potentially exposed to predators.

1.7.4 *Survival*

Diminished food resources near edges might also compromise survival of young and adults. Although this hypothesis has received little empirical support, some researchers propose that the Ovenbird's principal prey base, leaf litter invertebrates (Bent 1953, Stenger 1958), could be reduced by increased interspecific competition and/or leaf litter desiccation. The aggregation of organisms at the border of two distinct habitats may intensify competition for finite resources, resulting in competitive exclusion (Ambuel and Temple 1983, Temple and Cary 1988, Wiens 1989). Morse (1967) and Holmes and Sherry (1985) are among the number of researchers providing evidence for competitive exclusion in songbirds. Species that have evolved in forest interiors may be at a disadvantage when competing for food resources with species adapted to foraging in edge environments.

Although the Ovenbird does forage in low shrubs, 88% of its foraging occurs in the leaf litter (Holmes and Robinson 1988). Near edges, exposure of the forest floor to wind and solar radiation may desiccate the leaf litter and alter the humid microclimatic conditions on which the Ovenbird's prey base depends (Gibbs 1988, Wenny 1989). Burke and Nol (1998), working in Ontario woodlots surrounded by agriculture, provided the first evidence in support of this hypothesis. Ovenbird territories in large forest fragments contained slightly deeper leaf litter and 10 to 36 times greater prey biomass than territories in small fragments. The authors point out that edges in forest-dominated landscapes are less likely to cause Ovenbird food limitation due to more subtle microclimatic gradients and greater forest connectivity.

1.8 **Population Status**

Edge and area effects have been repeatedly implicated in local and regional population declines recorded for Ovenbirds and other neotropical migrants that dwell in forests (Robbins et al. 1989b, Hussell et al. 1992, Paton 1994). Where anthropogenically maintained edges are a predominant landscape feature, Ovenbird numbers have registered dramatic declines in recent decades (Askins et al. 1990, Ambuel and Temple 1982, Wander 1985). Over the same period, significant increases are reported in eastern Canada and northern New England, where old field succession and forest maturation are converting much of the land area to Ovenbird habitat (Robbins et al. 1986, Holmes et al. 1986, Hagan et al. 1992). Breeding Bird Survey (BBS) data show that temporal variation accompanies geographic variation in Ovenbird population trends. For all BBS routes combined, Ovenbirds increased by an annual average of 0.6% between 1966 and 1988, but in the last ten years of that period showed an overall decrease of 1% per year (Sauer and Droege 1992). Declines have been concentrated at the periphery of the Ovenbird breeding range, while increases have persisted toward its center (Van Horn and Donovan 1994). This pattern suggests that high quality habitat at the core of the Ovenbird breeding range acts as a population source supplying population sinks, distributed around the range's periphery (Pulliam 1988). Porneluzi et al. (1993), Donovan et al. (1995), and Robinson et al. (1995) have provide strong evidence for the application of the source-sink model to Ovenbirds.

1.9 **Ovenbirds in Forested Landscapes**

If Ovenbird populations are indeed structured in this manner, conservation of population sources is critical. Drawing on data from agricultural landscapes, Thomas (1994) argued that harvesting activity in the midst of high quality habitat threatens the Ovenbird's status. However, data from agricultural systems may be of limited use in predicting harvest effects in extensively forested landscapes (Hagan et al. 1996, King et al. 1996, Sabine et al. 1997). First, increasing regional forest cover ameliorates edge

effects on Ovenbird abundance (Robbins et al. 1989a, Porneluzi et al. 1993) and pairing success (Van Horn et al. 1995). In addition, brood parasitism (Robinson et al. 1995, Donovan et al. 1995) and nest predation (Andren 1985, Robinson et al. 1995) appear to diminish as forest cover increases. To date, information directly related to silvicultural effects on Ovenbirds remains limited. Nonetheless, results from silvicultural settings, interpreted with an appreciation for the Ovenbird's sensitivities in agricultural environments, can aid in the design of future research.

1.9.1 *Abundance and Pairing Success*

Small-scale clearcutting in extensive oak-hickory woodlands of Missouri did not reduce Ovenbird numbers (Thompson et al. 1992). With 20% of the forest cover in early successional stages, managed forests contained Ovenbird densities comparable to intact reserves. A similar experiment in New Hampshire yielded a different result (Welsh and Healy 1993). Ovenbirds were reduced in direct proportion to the amount of altered habitat. The fact that Ovenbird densities were unchanged in mature portions of the managed area suggests that numbers responded to an area effect, rather than edge effects. Yahner (1997) also discounted a negative effect of clearcut edges on abundance, reporting Ovenbirds were common in 100m x 100m uncut forest blocks, surrounded by 8-17 year-old clearcuts in Pennsylvania.

In separate studies, King et al. (1996, 1997) demonstrated that the distribution of Ovenbird territories adjacent to small (<12 ha) New Hampshire clearcuts did not exhibit edge aversion. Furthermore, they provided evidence in support of Kroodsma (1982), who proposed that, in some cases, perceived edge aversion may be a function of geometry; non-rectangular territories, in which song perches are centrally concentrated, favor detection of males away from a habitat boundary. Their data are also consistent with Thompson's (1993) computer simulation of Ovenbird response to clearcutting, wherein edge effects had only a small impact on population levels.

Although not explicitly examined, edge effects were not apparent in isolated forest fragments (2.5-38.5 ha) within a New Brunswick silvicultural mosaic (Sabine et al. 1997). There, mature forest patches surrounded by young (<15 yr) regenerating forest contained Ovenbirds in equal or insignificantly lower densities compared to nearby, contiguous forest. In the same study, pairing success was similar in both fragments (84%) and controls (86%). In a Connecticut forested landscape, another area-sensitive ground nester, the Worm-eating Warbler (*Helmitheros vermivorus*), paired successfully in large and small forests (Gale et al. 1997). These findings seem to contradict results from an industrial forest in Maine, where Hagan et al. (1996) reported exceptionally high Ovenbird densities and low pairing success in forest fragments. However, the Maine study occurred immediately following harvest, before post-disturbance crowding had subsided. The authors suggested that the relatively low pairing success (53% in fragments vs. 80% in reserve areas) was due to male behavioral dysfunction associated with over-saturation. For example, abnormally high densities may compromise the ability of males to defend territories (Hagan et al. 1996). The study lacked behavioral and detailed territory data to support this proposition. The importance of testing for post-harvest behavioral effects in remnant forest will be discussed further on. First, it is valuable to consider the only Ovenbird study to date (King et al. 1996) which specifically considered the influence of clearcut edges on male pairing success.

In New Hampshire forests adjacent to recent (<6 yr) clearcuts, Ovenbirds within the first 200m of the edge were just as likely to find mates as those settling 200m to 400m in the interior (King et al. 1996). Over two years, pairing success in the two distance classes averaged 89%. As well, edges did not influence the proportion of pairs fledging young, a result supported by data on Worm-eating Warblers (Gale et al. 1997). Although reproductive output did not vary with distance from the clearcut, edge-dwelling Ovenbirds had lower nest survival than interior conspecifics (King et al.

1996). Predation was largely responsible for the difference. Nonetheless, Ovenbirds at the edge maintained comparable productivity by renesting.

1.9.2 *Predation*

King et al.'s (1996) discovery of high predation near edges in a forested landscape is consistent with two previous artificial nest experiments (Chasko and Gates 1982, Small and Hunter 1988). However, most artificial nest studies in extensively forested regions (e.g. Angelstam 1986, Ratti and Reese 1988, Bayne and Hobson 1997, Cotterill 1996) have shown no edge effect. Two of these (Bayne and Hobson 1997, Cotterill 1996) were performed in Canada's boreal mixed-wood forest. In Minnesota mixed forests, research on natural nest predation also showed no edge influence on predation (Hanski et al. 1996). Such studies provide valuable support to artificial nest experiments, whose results do not directly reflect true predation (Haskell 1995).

1.10 A New Methodological Approach

The research reviewed thus far identifies important variables in determining effects of upland timber harvest on Ovenbirds breeding in riparian forests. The independent variable of concern is buffer strip width, as it relates to area and the edge:area ratio. Abundance is an obvious, and pertinent dependent variable, but is of limited value without complementary indices. Productivity data are most desirable, but the time required to find and monitor Ovenbird nests would severely limit the number of buffer replicates and, therefore, the study's credibility. The use of pairing success as an index of reproductive capacity represents a promising alternative. Indeed, combining measures of abundance and pairing success has been the approach favored by pioneers of Ovenbird research in silvicultural settings. Still, the first among them (Hagan et al. 1996) recognized the need for a more informative methodological approach. They proposed behavioral observation, a technique commonly disregarded by songbird conservation biologists. Records of territorial behavior, they argued, might reveal mechanisms underlying effects of harvesting.

To date, no research has addressed individual behavioral responses to the establishment of clearcut edges. Rectifying this oversight in an Ovenbird study presents a special challenge. Although vocally conspicuous, male Ovenbirds are cryptically colored and frequently retreat from human observers (Semenchuk 1992, pers. obs.). The literature's lack of a daily time budget for Ovenbirds (Van Horn and Donovan 1994) reflects the difficulty of studying their behavior. Nonetheless, the most observable Ovenbird activities (songs, chips, male-male chases) present a valuable research opportunity. Males use these behaviors to establish and maintain territories, which are of fundamental, ecological importance.

1.10.1 *The Significance of Territories*

For breeding songbirds, the territory is a critical element of reproductive success. Schoener (1968) reviewed the proposed functions of territories and identified nine categories of benefits to avian territory-holders.

1. *advantages accruing from familiarity with the environment*
2. *advantages of prior ownership in aggressive encounters*
3. *protection of nest and nest site*
4. *prevention of epidemics by spacing birds apart*
5. *reduction of loss to predation for cryptic species*
6. *prevention of inbreeding*
7. *facilitation of pair formation and maintenance*
8. *prevention of interference with reproductive activities*
9. *advantages arising from the restriction which territorial behavior imposes on the number of individuals using a limited food resource*

The relative significance of each proposed function varies among species according to different life history strategies (Krebs 1971, Wilson 1975). Regardless of the exact benefits, a territory's value under a given set of conditions might be expected to vary with changes in its size, shape, position, or vegetation structure. Theoretically, pronounced changes are capable of influencing reproductive success.

Territory features are responsive to habitat geometry (Krebs 1971, Wiens 1973, MacClintock et al. 1977, Kroodsma 1982, Seastedt and MacLean 1979) and conspecific density (Grant 1968, Krebs 1971, Barlow 1974, Morse 1976, Wiens et al. 1985, Wenny et al. 1993). Therefore, the linearization of Ovenbird habitat and the

possibility of short-term density effects (Darveau et al. 1995, Hagan et al. 1996) justify a close examination of Ovenbird territories in riparian buffer strips. The relationship between avian territory characteristics and environmental or population features is fertile ground for research (Wiens et al. 1985, Hagan et al. 1996). To my knowledge, no such investigation has been performed in buffer strips or in managed forests.

Below, I describe four possible scenarios in which changes in habitat geometry or Ovenbird density might influence territory characteristics. I also discuss potential reproductive consequences. These scenarios are organized by the four territory characteristics of concern.

Scenario1 - Size

Territories shrink to maintain defense benefits of naturally circular to moderately elliptical shape (Verner 1977, Zach and Falls 1978), while remaining within buffer strip boundaries. Avian territories may contain more food resources than required (Carrick 1972) and are therefore somewhat compressable (Huxley 1934). If territory compression is associated with crowding, high territory patrol and defense costs may be incurred. Disproportionate investment in territory maintenance may impede feeding of young and mate-guarding. Males face higher risks of cuckoldry in small, densely packed territories than in larger ones (Moller 1990).

Scenario 2 - Shape

Territories elongate to maintain constant size and conform to the configuration of the buffer strip. Maintaining long, thin territories is metabolically more expensive than defending compact territories since defense cost is related to the mean distance between points in the territory (Verner 1977). However, if elongated territories are immediately bounded by "hard edges" (e.g. lake, clearcut), they may experience low intruder pressure (Stamps et al. 1987). Reduction in intruder pressure could effectively nullify the added expense of territory elongation.

Scenario 3 - Position

Territories shift toward the water to maintain circularity and size. Possible consequences include: (a) increased exposure to the concentrated, riparian complex of predators and brood parasites, (b) elevated interspecific competition, and (c) change in vegetation structure characteristic of upslope territories (see 4).

Scenario 4 - Vegetation structure

Territories include atypical structural qualities. This scenario may follow Scenario 3. As previously discussed, vegetation at the land-water ecotone is often uniquely structured. Differences in structure between down- and up-slope territories may give rise to differences in the composition and/or availability of invertebrate prey (Smith and Shugart 1987). Females, which are thought to use habitat structure as a mate-selection cue (Zimmerman 1966, Smith and Shugart 1987, Van Horn 1990) could be less likely to pair with males situated in differently structured habitat. Since females disperse more widely than males, they may pass over philopatric, buffer-dwelling males for up-slope mating opportunities.

A combination of scenarios 1-4 may occur with the response probability related to buffer width. These and other potential effects of upland timber harvest would escape detection without detailed territory maps derived from focal observations.

1.11 Conclusion

Riparian forests are unique ecosystems generally characterized by high primary productivity and structural complexity. They are valued for their role in protecting water quality and aquatic habitat. A wide variety of aquatic, terrestrial, vertebrate, and invertebrate animal species utilize riparian forests, a significant proportion in a dependent capacity. In general, riparian forests feature high measures of wildlife density, species richness, and species diversity. This is true for the avifauna in most areas studied to date, though not in others. Regional differences are attributed to variably pronounced structural gradients from the water's edge to the upland.

In forests managed for timber production, the retention of riparian woodlands in buffer strips may result in bird species turnover, most notably the substitution of forest-dwelling birds with edge-adapted species. The Ovenbird is among several species reported to require substantial buffer widths, yet there is insufficient data to direct conservation efforts. The few, community-level studies that include information on Ovenbirds in buffer strips feature low replication and inconsistent results.

Fortunately, studies performed in other contexts provide valuable information concerning Ovenbird habitat associations and Ovenbird sensitivity to human activity. Ovenbirds are associated with upland forest throughout their breeding range and in much of their winter habitat. Those breeding in agricultural landscapes show low abundance, pairing success, and productivity near edges. These effects may be ameliorated by high regional forest cover. Early indications from extensively forested, silvicultural landscapes show less pronounced edge effects on Ovenbirds.

In riparian buffer strips, width is clearly an important variable. How wide must buffers be to conserve the Ovenbird and other area-sensitive species? If a certain width maintains Ovenbird numbers, is it sufficient to support characteristic pairing levels and normally configured territories? Abundance, pairing success and detailed territory data are required to address these questions. I collected all three in an effort to evaluate the conservation potential of buffer strips of varying width. Specifically, I investigated short-term effects of upland timber harvest on Ovenbirds in 20m, 100m, and 200m buffer strips (Chapter Two), and weighed management options with respect to their potential influence on forest songbirds (Chapter Three).

I hypothesized that Ovenbird sensitivity to upland timber harvest is inversely related to buffer strip width, such that 20m buffer strips represent the least suitable habitat, 100m buffers represent intermediate suitability, and 200m buffers provide the most suitable habitat. I predicted the following harvest effects.

1. In 20m buffer strips, Ovenbirds would be absent.

2.In 100m buffers:
a. Ovenbird numbers would be reduced;
b. Ovenbird territories would be configured differently than before harvest;
c. male Ovenbirds would have diminished pairing success.

3. In 200m buffers, there would be no detectable effect of harvest on Ovenbird abundance, territory characteristics, or pairing success.

The Terrestrial and Riparian Organisms, Lakes, and Streams Project (TROLS), administered by the University of Alberta Department of Biological Sciences in association with industry cooperators, designed the experimental manipulation and provided logistical support necessary to test these predictions. TROLS employs large-scale experimental research to develop a scientific basis for riparian forest management. The program involves the work of hydrologists, biogeochemists, aquatic ecologists, forest ecologists, and waterfowl, mammal, and songbird biologists. The collaborative approach affords the infrequent, but vital opportunity for disciplinary integration. I urge readers to consider the next chapter's findings in the context of other TROLS research.

1.12 **Literature Cited**

Alberta Environmental Protection. 1996. The Status of Alberta's Timber Supply, Edmonton, AB.

Alberta-Pacific Forest Industries, Inc. 1993. Timber Harvest Planning and Operating Ground Rules, Boyle, AB.

Ambuel, B., and S. A. Temple. 1982. Songbird populations in southern Wisconsin forests: 1954 and 1979. Journal of Field Ornithology 53:149-158

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Anderson, P. H., M. W. Lefor, and W. C. Kennard. 1980. Forested wetlands in eastern Connecticut: their transition zones and delineation. Water Resources Bulletin 16:248-255.

Anderson, S. H., K. Mann, and H. H. Shugart, Jr. 1977. The effect of transmission-line corridors on bird populations. American Midland Naturalist 97:216-221.

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794-804.

Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pp. 225-255 *in* L. Hansson, L. Fahrig, and G. Merriam (eds.), Mosaic Landscapes and Ecological Processes, Chapman and Hall, London.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47:365-373.

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7:1-57.

Barlow, G. W. 1974. Hexagonal territories. Animal Behavior 22:876-878.

Bayne, E., and K. Hobson. 1997. Artificial nest predation dynamics along a forest fragmentation gradient: a preliminary analysis. Journal of Sustainable Forestry 5:263-278.

Bent, A. C. 1953. Life Histories of North American Wood Warblers. United States National Museum, Bulletin 203, Washington, D.C.

Brode, J. M., and R. B. Bury. 1984. The importance of riparian systems to amphibians and reptiles. Pp. 30-36 *in* R. E. Warner and K. M. Hendrix (eds.), California Riparian Ecosystems: Ecology, Conservation and Productive Management, University of California Press, Berkeley.

Budd, W. W., P. L. Cohen, P. R. Saunders, and F. R. Steiner. 1987. Stream corridor management in the Pacific Northwest: I. Determination of stream-corridor widths. Environmental Management 11:587-597.

Bull, E. L. 1978. Specialized habitat requirements of birds: snag management, old growth, and riparian habitat. Pp. 74-82 *in* R. M. DeGraaf (tech. Coord.), Workshop on nongame bird habitat management in the coniferous forests of the western United States. US Forest Service General Technical Report PNW-64, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Burgess, C. 1997. Forested landscape patterns in the western boreal mixedwood forest of Alberta: riparian forests, fire history, canopy composition and topography. M.S. thesis. University of Alberta, Edmonton.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115:96-104.

Carrick, R. 1972. Population ecology of the Australian black-backed magpie, royal penguin, and silver gull. Pp. 41-99 *in* Population Ecology of Migratory Birds: A Symposium. US Department of the Interior Wildlife Research Report No. 2, Washington, D.C.

Castelle, A. J., C. Conolly, M. Emers, E. D. Metz, S. Meyer, M. Witter, S. Mauermann, T. Erickson, and S. S. Cooke. 1992. Wetland Buffers: Use and Effectiveness. Washington Department of Ecology Publication No.92-10. Olympia, WA.

Chapman, L., L. B. Miller, and D. J. McQueen. 1996. Riparian zones as corridor, habitat and buffer: a preliminary literature review. York University, Toronoto.

Chaney, E., W. Elmore, and W. S. Platts. 1990. Livestock grazing on western riparian areas. US Environmental Protection Agency, Washington, D.C.

Chasko, G. G., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. Wildlife Monographs 82.

Collins, S. L., F. C. James, and P. G. Risser. 1982. Habitat relationships of wood warblers (Parulidae) in northern central Minnesota. Oikos 39:50-58.

Cotterill, S. E. 1996. Effect of clearcutting on artificial egg predation in boreal mixedwood forests in north-central Alberta. M.S. thesis, University of Alberta, Edmonton.

Cross, S. P. 1985. Responses of small mammals to forest riparian perturbations. Pp. 269-276 *in* R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H.

Hamre (tech. Coords.), Riparian Ecosystems and Their Management: Reconciling Conflicting Uses. US Forest Service General Technical Report RM-120, Rocky Mountain Research Station, Fort Collins, CO.

Darveau, M., P. Beauchesne, L. Belanger, J. Huot, and P. LaRue. 1995. Riparian forest strips as habitat for breeding birds in the boreal forest. Journal of Wildlife Management 59:67-78.

Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural preserves. Biological Conservation 7:129-146

Donovan, T. M., F. R. Thompson, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in reproductive sources and sinks. Conservation Biology 9:1380-1395.

Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy 71:14-23.

Emmerich, J. M., and P. A. Vohs. 1982. Comparative use of four woodland habitats by birds. Journal of Wildlife Management 46:43-49.

Gale, G. A., L. A. Hanners, and S. R. Patton. 1997. Reproductive success of Worm-eating Warblers in a forested landscape. Conservation Biology 11:246-250.

Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in New Jersey. Auk 93:356-364.

Gates, J. E., and N. R. Giffen. 1991. Neotropical migrant birds and edge effects at a forest-stream ecotone. Wilson Bulletin 103:204-217.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Gentry, R. M. 1989. Variable mating success of the Ovenbird (*Seiurus aurocapillus*) within remnant forest tracts of central Missouri. M.A. thesis, University of Missouri, Columbia.

Gibbs, J. P. 1988. Forest fragmentation, mating success, and the singing behavior of the Ovenbird (*Seiurus aurocapillus*) and Kentucky warbler (*Oporornis formosus*) in central Missouri. M. A. thesis, University of Missouri, Columbia.

Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conservation Biology 2:193-196.

Gibbs, J. P., and D. G. Wenny. 1993. Song output as a population estimator: effect of male pairing status. Journal of Field Ornithology 64:316-322.

Grant, P. R. 1968. Polyhedral territories of animals. American Naturalist 102:75-80.

Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. American Midland Naturalist 129:288-300.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective on riparian zones. Bioscience 41:54-551.

Hagan, J. M., III, T. L. Lloyd-Evans, J. Atwood, and D. S. Wood. 1992. Long-term changes in migratory landbirds in the northeastern United States: evidence from migration capture data. Pp. 115-130 *in* J. M. Hagan and D. W. Johnston (eds.), Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, D.C.

Hagan, J. M., III, W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188-202.

Hann, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bulletin 49:145-237.

Hanski, I. K., T. J. Fenske, and G. J. Niemi. 1996. Lack of edge effect in nesting success of breeding birds in managed forested landscapes. Auk 113:578-585.

Harris, L. D. 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. The University of Chicago Press, Chicago.

Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology 9:1316-1318.

Hawrot, R. Y., and G. J. Niemi. 1996. Effects of edge type and patch shape on avian communities in a mixed conifer-hardwood forest. Auk 113:586-598.

Henein, K. M., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology 4:157-170.

Holmes, R. T., and S. K. Robinson. 1988. Spatial patterns, foraging tactics, and diets of ground foraging birds in a northern hardwoods forest. Wilson Bulletin 100:377-394.

Holmes, R. T., and T. W. Sherry. 1986. Dispersion patterns and habitat responses of birds in northern hardwood forests. Pp. 283-309 *in* M. L. Cody (ed.), Habitat Selection in Birds, Academic Press, Inc., New York.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1985. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 56:201-220.

Hooper, S. T. 1991. Distribution of songbirds in riparian forests of central Maine. M.Sc. Thesis, University of Maine, Orono.

Hornbeck, J. W., C. W. Martin, and C. T. Smith. 1986. Protecting forest streams during whole tree harvesting. Northern Journal of Applied Forestry 3:97-100.

Hussell, D. J. T., M. H. Mather, and P. H. Sinclair. 1992. Trends in numbers of tropical and temperate-wintering migrant landbirds in migration at Long Point, Ontario, 1961-1988. Pp. 101-114 *in* J. M. Hagan III and D. W. Johnston (eds.), Ecology and Conservation of Neotropical Migrant Land Birds. Smithsonian Institution Press, Washington, D.C.

Huxley, J. S. 1934. A natural experiment on the territorial instinct. British Birds 27:270-277.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology 67:629-637.

Johnson, E. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. Endangered habitats: a concept. Pp. 68-80 *in* R. R. Johnson and D. A. Jones (eds.), Importance, Preservation, and Management of Riparian Habitat: A Symposium. US Forest Service, Fort Collins, CO.

Johnson, W. N., and P. W. Brown. 1990. Avian use of a lakeshore buffer strip and an undisturbed lakeshore in Maine. Northern Journal of Applied Forestry 7:114-117.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in a forested landscape. Conservation Biology 101:1380-1386.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. Wilson Bulletin 109:239-245.

Krebs, J. R. 1971. Territory and breeding density in the great tit. Ecology 52:2-22.

Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. Journal of Applied Ecology 19:361-370.

Kroodsma, R. L. 1984. Effect of edge on breeding forest bird specis. Wilson Bulletin 96:426-433.

Krueper, D. J. 1992. Effects of land use practices on western riparian ecosystems. Pp. 321-330 *in* D. M. Finch and P. W. Stangel (tech. coords.), Status and Management of Neotropical Migratory Birds: A Symposium, Estes Park, Colorado, Sept. 21-25. U.S. Forest Service, Fort Collins, CO.

Lack, D., and P. Lack. 1972. Wintering warblers in Jamaica. Living Bird 11:129-153.

LaRue, P., L. Belanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. Canadian Journal of Forest Research 25:555-566.

Lein, M. R. 1980. Display behavior of Ovenbirds. I. Song vocalizations. Wilson Bulletin 92:312-329.

Lein, M. R. 1981. Display behavior of Ovenbirds (*Seiurus aurocapillus*): II. Non-song vocalizations. Wilson Bulletin 93:21-41.

Lynch, J. F., and D. F. Whigham. 1978. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28: 287-324.

MacClintock, L., R. F. Whitcomb, and B. L. Whitcomb. 1977. Island biogeography and habitat islands of eastern forest. II. Evidence for the value of corridors and minimization of isolation in the preservation of biotic diversity. American Birds 31:6-12.

Machtans, C. S. 1996. Riparian buffer strips: their value as habitat and movement corridors for songbirds in the boreal mixedwood forest of Alberta. M.S. thesis, University of Alberta, Edmonton.

Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology 10:1366-1379.

Martin, C. W., and R. S. Pierce. 1980. Clearcutting patterns affect nitrate and calcium in New Hampshire streams. Journal of forestry 778:268-272.

McGarigal, K., and N. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. Journal of Wildlife Management 56:10-23.

Mills, G. S., J. B. Dunning, and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. Wilson Bulletin 103:468-482.

Moller, A. P. 1990. Changes in the size of avian breeding territories in relation to the nesting cycle. Animal Behaviour 40:1070-1079.

Morse, D. H. 1967. Competitive relationships between Parula Warblers and other species during the breeding season. Auk 84:490-502.

Morse, D. H. 1976. Variables affecting the density and territory size of beeding spruce woods warblers. Ecology 57:290-301.

Murray, N. L., and D. F. Stauffer. 1980. Nongame bird use of habitat in Central Appalachian riparian forests. Journal of Wildlife Management 59:78-88.

Naiman, J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3: 209-212.

Noss, R. F. 1992. Wildlife corridors. Pp. 43-68 *in* D. Smith and P. Hellmund (eds.), Ecology of Greenways. University of Minnesota Press, Minneapolis.

Ohmart, R. D., W. O. Deason, and C. Burke. 1977. A riparian case history: the Colorado River. Pp. 35-47 *in* R. R. Johnson and D. A. Jones (eds.), Importance, Preservation and Management of Riparian Habitat: A Symposium. US Forest Service, Fort Collins, CO.

Paton, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? Conservation Biology 8:17-26.

Plamondon, A. P., A. Gonzalez, and Y. Thomassin. 1982. Effects of logging on water quality: comparison between two Quebec sites. Pp. 49-70 *in* Hydrological Processes of Forested Areas: Proceedings of the Canadian Hydrology Symposium '82, National Research Council of Canada, Fredricton, NB.

Porneluzi, P., J. C. Bednarz, L. J. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. Conservation Biology 7: 618-622.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pp. 353-393 *in* A. Keast and E. S. Morton (eds.), Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and conservation. Smithsonian Institution Press, Washington, D.C.

Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management 52:484-491.

Robbins, C. S., D. Bystrak, and P. Geissier. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. US Fish and Wildlife Service Research Publication No. 157.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989a. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103: 1-34.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989b. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences 86:7658-7662.

Robinson, S. K. 1992. Population dynamics of breeding neotropical migrants in a fragmented Illinois landscape. Pp. 408-418 *in* J. M. Hagan in D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 167:1987-1990.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Sabine, D. L., A. H. Boer, and W. B. Ballard. 1996. Impacts of habitat fragmentation on pairing success of male Ovenbirds, *Seiurus aurocapillus*, in Southern New Brunswick. The Canadian Field-Naturalist 110:688-693.

Sauer, J. R., and S. Droege. 1992. Geographic patterns in population trends of neotropical migrants in North America. Pp. 26-42 *in* J. M. Hagan III and D. W. Johnston (eds.), Ecology and Conservation of Neotropical Migrant Land Birds. Smithsonian Institution Press, Washington, D.C.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914-1932.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.

Seastedt, T. R., and S. F. MacLean. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. Auk 96:131-142.

Semenchuk, G. P. 1992. The Atlas of Breeding Birds of Alberta. Federation of Alberta Naturalists. Edmonton.

Small, M. F., and M. L. Hunter, Jr. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76:62-

Small, M. F., and M. L. Hunter. 1989. Response of passerines to abrupt forest-river and forest-powerline edges in Maine. Wilson Bulletin 101:77-83.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68:695-704.

Spackman, S. C., and J. W. Hughes. 1995. Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. Biological Conservation 71:325-332.

Stamps, J. A., M. Buchner, and V. V. Krishnan. 1987. American Zoologist 27:307-325.

Stauffer, D. F., and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. Journal of Wildlife Management 44:1-15.

Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. Auk 75:335-346.

Stevens, L., B. T. Brown, J. M. Simpson, and R. R. Johnson. 1977. The importance of riparian habitat for migrating birds. Pp. 156-164 *in* Proceedings of the Symposium on Importance, Preservation, and Management of Riparian Habitat. U.S. Forest Service, Fort Collins, CO.

Suffling, R. H., B. Smith, and J. Dal Molin. 1982. Estimating past forest age and disturbance rates in north-western Ontario: a demographic approach. Journal of Environmental Management 14:45-56.

Swanson, F. J., G. W. Leinkaemper, and J. R. Sedell. 1976. History, physcal effects, and management implications of large organic debris in western Oregon streams. USDA Forest Service General Technical Report PNW-56, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Swift, B. L., J. S. Larson, and R. M. DeGraaf. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. Wilson Bulletin 96:48-59.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340-347.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, J. Verner. 1990. A Conservation Strategy for the Northern Spotted Owl, US Forest Service, Bureau of Land Management, Fish and Wildlife Service, and National Park Service, Portland, OR.

Thomas, R. G. 1994. Making Connections: Alberta's Neotropical Migratory Birds. Mono Congo Joint Venture, Calgary.

Thompson, F. R. III. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. Conservation Biology 7:325-333

Thompson, F. R., III, W. D. Dijak, T. G. Kulowiec, and D. A. Hamilton. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. Journal of Wildlife Management 56:23-30.

Triquet, A. M., G. A. McPeek, and W. C. McComb. 1990. Songbird diversity in clearcuts with and without a riparian buffer strip. Journal of Soil and Water Conservation 45:500-503.

Van Horn, M. A. 1990. The relationship between edge and the pairing success of the Ovenbird (*Seiurus aurocapillus*). M.A. thesis, University of Missouri, Columbia.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). No. 88 *in* A. Poole and F. Gill (eds.), Birds of North America. The Academy of Natural Science of Philadelphia, PA.

Van Horn, M. A., R. M. Gentry, and J. Faaborg. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. Auk 112:98-106.

Van Horne, B. 1983. Density is a misleading indicator of habitat quality. Journal Wildlife Management 47:893-901.

Van Miegroet, H., and D. W. Johnson. 1993. Nitrate dynamics in forest soils. Pp. 75-98 *in* T. P. Burt, A. L. Heathwaite, and S. T. Trudgill (eds.), Nitrate Processes, Patterns, and Management. John Wiley and Sons, New York.

Vandal, D., and J. Huot. 1985. Le milieu riverain sec: definition et importance comme habitat faunique. Ministere du Loisir, de la Chasse et de la Peche, Quebec.

Verner, J. 1977. On the adaptive significance of territoriality. American Naturalist 111:769-775.

Vickery, P. D., M. L. Hunter, and J. V. Wells. 1992. Is density an indicator of breeding success? Auk 109:706-710.

Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). Auk 110:759-768.

Wander, S. A. 1985. Comparative breeding biology of the Ovenbird in large vs. fragmented forests: implications for the conservation of neotropical migrant birds. Ph.D. dissertation, Rutgers University, New Brunswick, NJ.

Welsh, C. J. E., and W. M. Healy. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. Wildlife Society Bulletin 21:143-154.

Wenny, D. 1989. Population density and area requirements of three forest interior warblers in central Missouri. M.A. thesis, University of Missouri, Columbia.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection, and minimum area requirements of three forest interior warblers in central Missouri. Condor 95:968-979.

Whitfield, T. S., and R. J. Hall. 1997. Effect of timber harvest on aquatic and terrestrial communities within wetland-riparian ecosystems. Ontario Ministry of Natural Resources File Report 28.

Wiens, J. A. 1973. Interterritorial habitat variation in grasshopper and savannah sparrows. Ecology 54:877-883.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1985. Territory size variations in shrubsteppe birds. Auk 102:500-505.

Wiens, J. A. 1989. The ecology of bird communities. Cambridge University Press, Cambridge, UK.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Wilson, E. O. 1975. Sociobiology. Harvard University Press, Cambridge, MA.

Yahner, R. H. 1997. Long-term dynamics of bird communities in a managed forest landscape. Wilson Bulletin 109:595-613.

Zach, R., and J. B. Falls. 1978. Bivariate normal song territories in ovenbirds. Canadian Journal of Zoology 56:2088-2092.

Zimmerman, J. L. 1966. Polygyny in the Dickcissel. Auk 83:534-546.

Chapter Two

Ovenbirds in Riparian Buffer Strips: Short-term Response to Upland Timber Harvest in Alberta's Boreal Mixed-wood Forest

2.1 Introduction

Riparian forests, bordering wetlands, streams and lakes, perform a variety of important ecological functions. They buffer aquatic habitat from climatic extremes, moderate watershed discharge, and filter particulate and dissolved substances from runoff (Bormann and Likens 1979). Vegetation at the land-water ecotone is generally distinguished by high primary productivity (Johnson et al. 1977), species richness (Spackman and Hughes 1995), species diversity (Gregory et al. 1991), and structural complexity (Mills et al. 1991). Thus, riparian areas are unsurpassed as wildlife habitat by measures of abundance, richness, diversity, and degree of endemism (reviews in Budd et al. 1987, Chapman et al. 1996). The importance of riparian ecosystems to wildlife has been demonstrated for amphibians (Brode and Bury 1984 as cited by Chapman et al. 1996), mammals (Doyle 1990, Spackman and Hughes 1995), and birds (Gates and Giffen 1991, LaRue et al. 1995, but see McGarigal and McComb 1992).

In landscapes managed for forestry, riparian woodlands are retained in buffer strips, designed primarily to protect water quality (Martin and Pierce 1980, Hornbeck et al. 1986). Though little information exists to assess their habitat value (Johnson and Brown 1990, Darveau et al. 1995), buffers also act as wildlife reserves. Avian research in buffer strips indicates that cutting upland forest can result in short-term density increases (Darveau et al. 1995, Machtans 1996) and replacement of interior forest songbirds with edge-adapted species (Triquet et al. 1990, Johnson and Brown 1990, Darveau et al. 1995, Machtans 1996).

The Ovenbird (*Seiurus aurocapillus*) is a neotropical migratory warbler associated with the interior of extensive forest tracts (Wander 1985, Gibbs and Faaborg 1990, Villard et al. 1993). It occurs in predominantly deciduous, closed-canopy woodlands

that have reached 16-22m in height (Van Horn and Donovan 1994). It is among several species that have declined in riparian forests following upland timber harvest. For example, after clearcutting in Kentucky, Ovenbirds disappeared from a stream-side woodland measuring 15-23m in width (Triquet et al. 1990). In Alberta, Ovenbird abundance decreased in two 100m buffers following harvest (Machtans 1996). Research in Iowa suggested that Ovenbirds require a minimum buffer width of 175m (Stauffer and Best 1980). However, six years after upland clearcutting in Maine, numbers did not differ between a 70-100m buffer strip and an undisturbed riparian forest (Johnson and Brown 1990).

Low replication and inconsistency limit the value of these results to forest managers seeking to conserve species like the Ovenbird in riparian forests. Moreover, the abundance estimates, based on periodic point-count and spot-map records of singing males, may have been inaccurate. Because males with mates sing about one-third to one-half as often as those without (Lein 1981, Gibbs and Wenny 1993), previous research may have underestimated the number of paired males (Gibbs and Faaborg 1990, Gibbs and Wenny 1993). Even when accurate, density estimates do not necessarily reflect habitat quality (Van Horne 1983, Vickery et al. 1992). For example, during the post-harvest breeding season in Maine's industrial forest, male Ovenbirds packed into forest fragments, where the probability of mating was low (Hagan et al. 1996). The authors proposed that behavioral dysfunction, associated with over-crowding, may have resulted in territory breakdown and low pairing success.

Hagan et al. (1996) argued that habitat suitability assessments should utilize pairing and behavioral data to complement abundance information. Over the past decade, several other studies have used rates of Ovenbird pairing success to evaluate the quality of forest tracts in both agricultural (Gibbs and Faaborg 1990, Villard et al. 1993, Porneluzi et al. 1993, Van Horn et al. 1995, Burke and Nol 1998) and silvicultural landscapes (Sabine et al. 1996, King et al. 1996, Yahner 1997). However, to my

knowledge, no study has yet examined effects of timber management on songbird behavior. Behavioral information, especially that concerning territory characteristics, may be particularly valuable in determining the conservation potential of riparian buffer strips. Indeed, territories are fundamental elements of songbird breeding success (Schoener 1968, Verner 1977) which respond to changes in habitat geometry (Krebs 1971, Kroodsma 1982), and conspecific density (Morse 1976, Wiens et al. 1985). Compression, distortion, or adjustments in territory position could reduce the fitness of territory-holders in a variety of ways, including: prey base depletion, heightened interspecific competition, increased territory maintenance costs, and mating failure. Therefore, the size, shape and, position of Ovenbird territories in riparian forests warrant measurement before and after upland timber harvest.

The boreal mixed-wood forest of north-central Alberta provides opportune conditions for such an investigation. In this ecoregion, over 80,000km^2 of woodland have been leased to pulp and paper companies in recent years (Alberta Environmental Protection 1996). Management plans call for checkerboard clearcutting of stands dominated by trembling aspen (*Populus tremuloides*) in a two- to three-pass harvest regime. A minimum of ten years will separate passes while rotation lengths are projected to be 60-70 years. Next to lakes greater than 4ha, forest managers will maintain unharvested reserves in 100m-wide riparian buffer strips (Alberta-Pacific 1993). In many areas, forests over 60-70 years of age will be concentrated in these zones. Consequently, buffers may play a significant role in the long-term conservation of the region's native songbird community.

The suitability of buffer strips for Ovenbirds may depend on effects of riparian and clearcut edges on the species' distribution. Studies in forest patches surrounded by agricultural land have indicated that Ovenbird abundance is low near edges (MacClintock et al. 1977, Wenny 1989). This pattern has been upheld in riparian ecotones (LaRue et al. 1995, Hawrot and Niemi 1996), but not in areas adjacent to

clearcuts (King et al. 1996, 1997). In the boreal mixed-wood forest, the Ovenbird's response to buffer strip creation cannot be properly evaluated without addressing the independent influences of riparian and clearcut edges on its abundance. Therefore, I conducted a spot-mapping study of Ovenbird distribution in forests adjacent to lakes, next to clearcuts and at interior upland sites. I predicted that the abundance of Ovenbirds would be low within 100m of lakes compared to forest interiors. I expected Ovenbird numbers within 100m of clearcuts to be similar to those found in interior control sites.

In addition, I directly assessed the value of buffer strips to Ovenbirds in a pre- and post-harvest study with contemporary controls. I evaluated abundance data, detailed territory maps, and pair sightings to measure the short-term response of Ovenbirds to upland timber harvest in 20m, 100m, and 200m buffer strips. I hypothesized that the suitability of buffer strip habitat increases with width, such that 20m buffers represent the least suitable habitat, 100m buffers represent intermediate suitability, and 200m buffers provide the most suitable habitat relative to controls. I predicted the following harvest effects.

1. In 20m buffer strips, Ovenbirds would be absent.

2. In 100m buffers:
   a. Ovenbird numbers would be reduced;
   b. Ovenbird territories would be configured differently than before harvest;
   c. male Ovenbirds would have diminished pairing success.

3. In 200m buffers, there would be fewer detectable effects of harvest on Ovenbird abundance, pairing success, or territory characteristics.

2.2 **Methods**

2.2.1 *Description of Forest Type*

We conducted the research in the boreal mixed-wood forest of north-central Alberta, a low-relief mosaic of trembling aspen and balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*) and jackpine (*Pinus banksiana*) stands. Although forest cover dominates this ecoregion, shallow lakes, wetlands, roads,

cutblocks and seismic lines are also characteristic features. All study sites were located in 50-100 year-old forests, where aspen and balsam poplar comprised 60-100% of the canopy. To varying degrees, white spruce, white birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) were present in the subcanopy or as minor canopy components. Shrub species were heterogeneous in dispersion and structure, consisting primarily of prickly rose (*Rosa acicularis*), lowbush cranberry (*Viburnum edule*), wild red raspberry (*Rubus idaeus*), and Saskatoon berry (*Amelanchier alnifolia*). Flower, fern, grass, and moss species made up the ground vegetation, which typically ranged from 10% to 30% in cover.

2.2.2 *Site Locations*

Study sites were distributed among three research areas: Lac La Biche (LLB), South Calling Lake (SCL) and South Pelican Hills (SPH) (Fig.1). Each area contained three treatment lakes, with buffer strip widths of 20m, 100m and 200m . A fourth lake, isolated from clearcuts by at least 800m, served as a control (Fig. 2). This experimental design was developed by the TROLS (Terrestrial and Riparian Organisms, Lakes, and Streams) project at the University of Alberta, a multi-discliplinary investigation into effects of buffer width on terrestrial and aquatic ecosystems. During the winter of 1996-97, after the first field season, 3.6-39.5% (x = 18.5%) of the forest area within 800m of treatment lakes was harvested in a checkerboard fashion, creating two opposing, 400m-long buffers of the prescribed width. Unharvested blocks occurred adjacent to the remainder of riparian forest surrounding the lake. Harvest blocks, ranging in size from 11-38ha, retained approximately 0-5% standing, merchantable timber in small, scattered clumps. Combined, the 3 research areas contained 6 replicates of 100m and 200m treatments. Due to a harvesting error at one 20m site, we sampled 5 replicates of this width class. With 4 study sites located on each undisturbed lake (Fig. 2), riparian control replicates numbered 12.

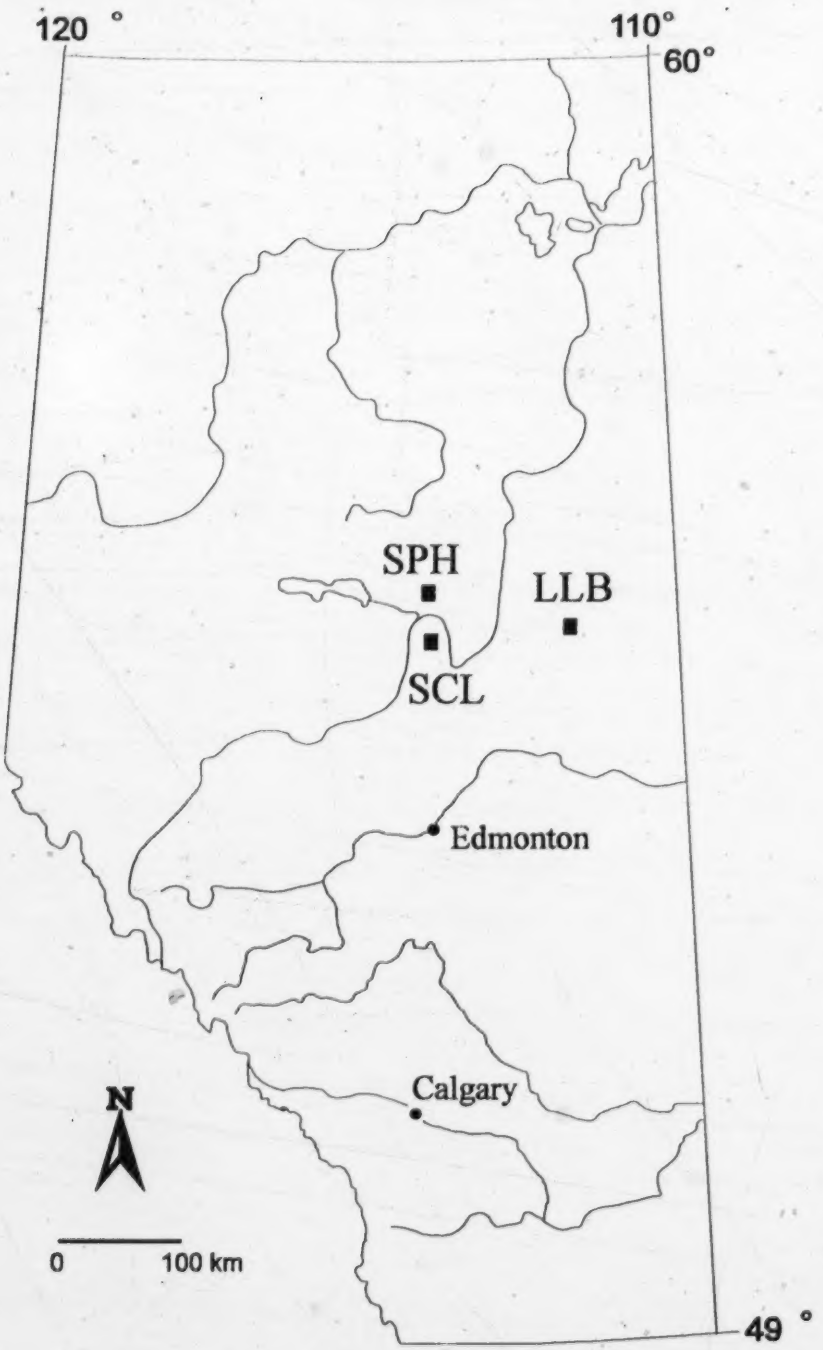


Figure 2.1. Location of TROLS research areas in Alberta, Canada.

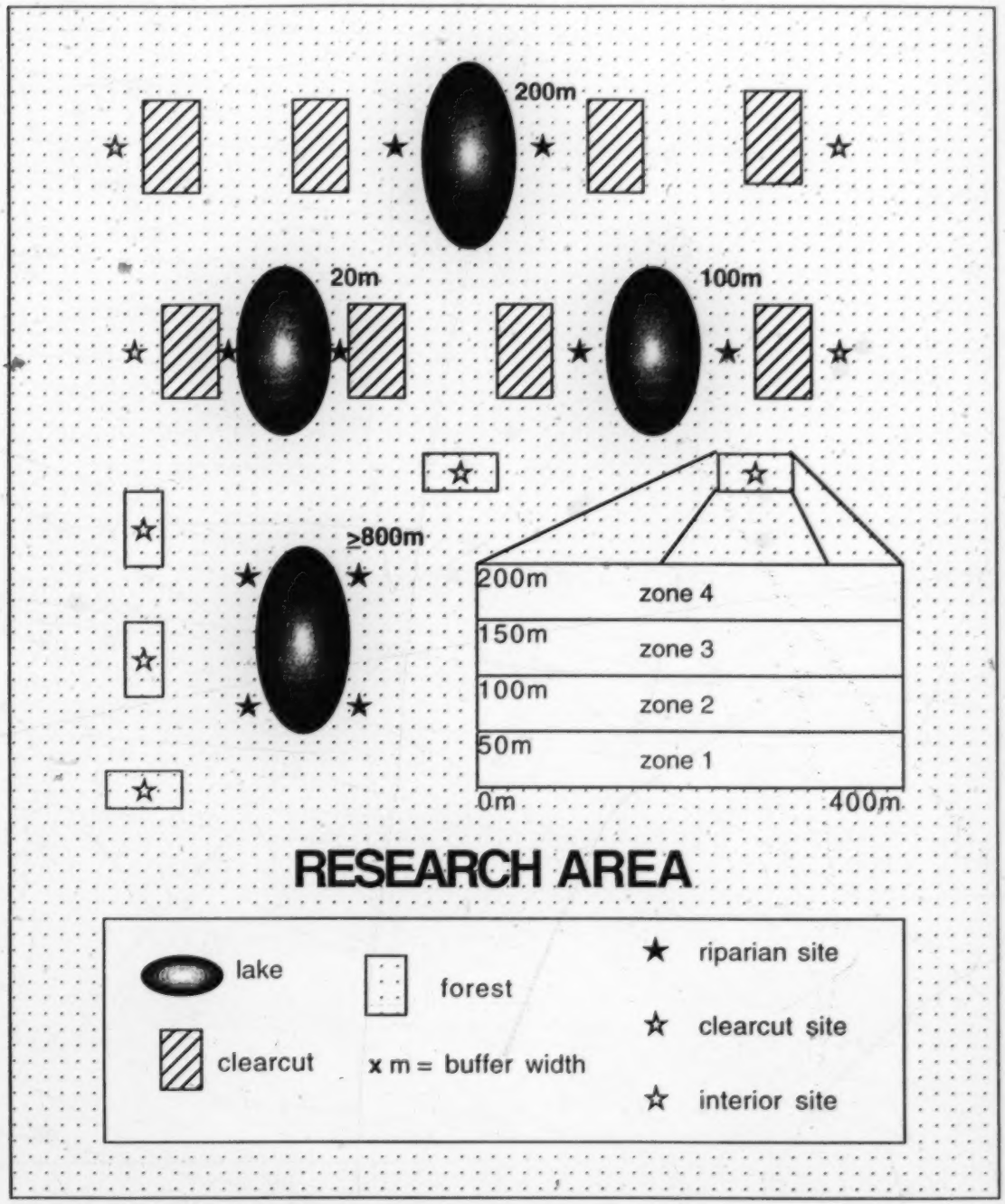


Figure 2.2. Schematic diagram of a single research area. Study sites, marked by stars, were divided into four 50m-wide zones for purposes of analysis. In riparian and clearcut sites, zone 1 bordered the lake and clearcut, respectively. In interior sites, zone 1 was randomly assigned. All study sites were 400m long; interior and clearcut sites and riparian sites situated next to the undisturbed (control) lake were 200m wide; width of other riparian sites was determined by buffer strip width.

Together, LLB and SCL contained 20 additional sites located in upland forests. Ten of these abutted 0-3 year-old clearcuts (hereafter "clearcut sites"), while the remaining 10 were reference sites isolated from lakes and clearcuts by over 250m (hereafter "interior sites"). Sampling of clearcut and interior sites helped to weigh the influence of cutblocks and lakes on Ovenbird distribution.

2.2.3 *Estimating Abundance*

During the breeding seasons before (1996) and after harvest (1997), we performed extensive spot-mapping to estimate Ovenbird abundance at all riparian study sites (after Bibby et al. 1992).[1] We surveyed the sites into 400m-long grids, composed of 50m square cells. We assigned a zone number to each row of cells (Fig. 2). A transect bisected each zone lengthwise with spot-map stations located at 50m intervals. Grids extended 100m upland at 20m and 100m lakes and 200m upland at 200m and control lakes. In most cases, we sampled a 50m periphery around each grid. The lower half of each control site (zones 1 and 2) was designated as a reference for 100m buffer strips. The entire control site (zones 1-4) served as a reference for 200m buffers. In 1996 and 1997, between 20 May and 4 July, each of several trained technicians sampled two grids per morning. We alternated observers, entry points and sampling sequence to minimize bias, and visited each site 6 times at 5 to 7-day intervals. We spot-mapped the full songbird community, at a rate of 30 minutes per transect, between sunrise and 11:00 a.m.

At upland interior sites and clearcut sites, we followed a similar protocol for 1997 only. For more efficient mapping of the focal species, we spot-mapped along 3 transects separated by 75m. This design deviated from the riparian site layout, 2-4 transects separated by 50m. The modified layout permitted an individual to map Ovenbirds, and 6 other species not discussed here, on 2-3 grids per morning. Otherwise, upland spot-mapping methods were the same as described for riparian sites.

[1] TROLS core technicians performed spot-mapping at riparian sites.

We compiled maps on transparent sheets and distinguished territories according to patterns of song perch clusters and counter-singing events. A territory was designated on the grid if the majority of song perches occurred within the grid's boundaries. If a given male's on-site and off-site song perches were equal in number, we drew a polygon around the points. Then, if the majority of a polygon's area overlapped the grid, it was considered on. If a minor portion of the polygon overlapped the grid, it was considered off. Rather than assign fractional values to territories, we assumed that the sum of partial territories excluded from counts equalled the sum of partial territories added. We confirmed the accuracy of this approach with detailed territory-maps, described below.

2.2.4 *Territory-mapping*

In order to measure territory characteristics we performed more intensive "territory-mapping" in a subset of riparian sites. We mapped territories at 13 sites in 1996 and 17 sites in 1997 (Table 2.1). Because Ovenbirds were not expected in 20m buffer strips after harvest, no territories in this width class were closely examined. However, each buffer width over 20m is represented by four to seven site replicates.

Table 2.1. Distribution of riparian sites in which intensive territory-mapping was conducted.

Research area	Buffer Class	1996	1997
LLB	100m	2	5 *
	200m	2	2
	control	3	3
SCL	100m	2	2
	200m	2	2
	control	2	3
TOTAL		13	17

* 3 added buffer strips abutted 1-2 year-old clearcuts

Each year, between 20 May and 12 July, we visited sites 6-8 times at an average interval of 7 days (range = 5-10). We began our observations one-half hour before dawn, with a 20-30 minute Ovenbird survey. While walking a central transect through a strip's interior, we noted the approximate position of all males singing on the grid or from adjacent areas. In this manner, we were able to determine where to concentrate our attention during the less active, mid-morning hours. We then targeted individual males and mapped their activity, in sequence, for up to an hour. Late in the season, as observable activity subsided, the maximum observation period was abbreviated to 30 minutes. If a focal male went undetected for 15 minutes, we turned our attention to a neighboring territory and returned when time allowed. We alternated the sequence of focal observations with each site visit so that time of day would not bias results. We ceased observations at either 11:00 a.m. or after one hour without detections.

During the late morning and early afternoon hours, we lured territorial males into 12m x 2m mist nets with a decoy and the broadcast of recorded Ovenbird song. We noted recaptures and banded newly captured individuals with unique, two-leg combinations of three plastic color-bands and one Canadian Wildlife Service aluminum band. Color-bands on one-third of the males (34 of 102) helped us distinguish between neighboring males.

At season's end, I compiled and analyzed maps of Ovenbird movement, interactions, song perches, and simultaneous singing episodes in order to delineate each territory. I digitized each individual's song perches in the Geographical Resources Analysis Support System (GRASS), a geographic information system (GIS) developed by the U.S. Army Construction Engineering Research Laboratories. In order to identify a minimum number of song perches necessary to delineate a territory, I analyzed the 13 territories which had over 85 mapped song perches. For each territory, I randomly subsampled clusters of song perches in 10-perch increments, beginning with 20 perches (i.e. 20, 30, 40. . .). Each cluster was replaced before a new cluster

was drawn from the total number of song perches. Next, I drew a minimum convex polygon (MCP) enclosing each cluster. I then graphed polygon area vs. number of song perches and observed that MCP sizes increased up to, and stabilized beyond, the 50-perch threshold (see Appendix 1 for more details). I therefore concluded that a MCP drawn around 50 song perches, mapped during 5 or more visits, adequately described Ovenbird territories. For the 13 thoroughly mapped birds, 50-perch MCPs constituted, on average, 0.87 (SE = 0.03) and 0.85 (SE = 0.03) of the total utilized areas in 1996 and 1997, respectively.

Next, I drew MCPs around 50 randomly subsampled song perches for all territories that had a minimum of 50 perches mapped (n = 31 in 1996, n = 42 in 1997). For each of these, GRASS calculated the area (ha) and a circularity index [(0.282 x perimeter)/(area)$^{1/2}$] that varies between 1.0 for a circle and infinity for an infinitely long and narrow shape. An index of 1.12 represents a square. With GRASS, I also measured each polygon's minor and major axis lengths.

I measured territory position in two ways: first, relative to the riparian edge and second, according to the area overlapping the sampling grid's 50m zones. For each 50m zone in the 100m, 200m, and control classes, I calculated direct and proportional measures of overlap. The former variable represented the mean area of zone x occupation per mapped bird, while the latter represented a mean percentage of each bird's territory occurring in zone x.

Intensively mapped territories were awarded values in increments of 0.25 according to the degree of grid overlap. These refined estimates were possible due to the high resolution of territory-maps compared to that of spot-maps. The more sensitive approach allowed us to verify results derived from the extensive spot-mapping protocol.

2.2.5 *Vegetation Analysis*

In order to determine whether the lake-side habitat in zone 1 differed from adjacent zones, we gathered information on seven structural variables, deemed important in previous Ovenbird habitat research (Van Horn and Donovan 1994).[2] They included: tree basal area, canopy height, canopy cover, shrub height, shrub cover, herb cover, and litter depth. All vegetation plots were situated 5m from spot-mapping stations and were separated by a minimum of 100m. They measured 20m x 5m and were oriented along the grid's length. Zone 1 vegetation plots (n = 36) were located 25m from the riparian edge and were evenly divided among 12 of the intensively mapped grids. From the same 12 grids, we randomly selected one vegetation plot from within each of 36 Ovenbird territories mapped in 1996. Each of these plots was located in zones 2-4. We used data from the pre-harvest year only, to minimize year and treatment effects.

We measured basal area (BA) of trees by first enumerating all live stems over 2m high in each of 5 dbh classes (<8cm, 8-1 cm, 15-23cm, 23-28cm, and 28-36cm) and then calculating $BA = \Sigma (\pi r^2_i n_i)$ where r_i = the median radius at breast height within class i and n_i = the number of representative stems in class i. For canopy height, we measured a characteristic canopy tree with a clinometer. We measured canopy cover as the mean of two convex densiometer readings, taken at opposite corners of the vegetation plot. We randomly nested a 1.78m-radius, circular plot ($10m^2$) within the vegetation plot, and visually estimated shrub and herb cover. We calculated shrub height (SH) as $SH = \Sigma(h_i p_i/p_i)$, where h_i = the height of species i, and p_i = the percent cover of species i. Litter depth was calculated as the mean of 4 measurements from pits dug at each corner of the vegetation plot.

2.2.6 *Determining Pairing Success*

We performed focal observations of males to determine pairing success, using methods modified from previous Ovenbird research. On intensively mapped sites, we

[2] TROLS core technicians collected the vegetation data.

tracked individual males for up to 90 minutes over the course of the season (May 20 to July 12) (Gibbs and Faaborg 1990, Villard et al. 1993). Track time accumulated when the focal individual was in sight or in continuous song at a distance <30m from the observer (Hagan et al. 1996). In this time, males tolerating a non-vocal conspecific within a distance of 10m were considered paired. A status of paired was also assigned when a female's high *tsip* vocalization was heard in the presence of a singing male (Sabine et al. 1996). This distinctive courtship call (Lein 1980) indicates the female's association with the male (Van Horn and Donovan 1994). Males not observed with a female after 90 minutes were considered unpaired. Those tracked for under 90 minutes were classified as unknown.

To avoid inaccurate pairing status determination, we applied three precautionary standards. First, we tracked males for no more than 30 minutes during the first round of observations (May 20 to May 27), when some females may not yet have selected mates. Second, during each succeeding sampling effort (n=5-7), we tracked for a maximum time of 60 minutes, no more than 30 minutes continuously. Finally, males had to have been tracked for at least 60 minutes before the incubation phase, a period in which pairs are rarely observed together. In two seasons, 67 of 78 known pairs (86%) were identified in 45 minutes of track time, while 76 (97%) percent were observed within 75 minutes. These figures validate 90 minutes as a reliable threshold for pairing status determination.

2.2.7 *Data Analysis*

I used paired and unpaired t-tests, Wilcoxon signed-ranks and Mann-Whitney U tests, as appropriate, to compare abundance and territory variables between treatment and control groups and between years. I used a one-way ANOVA with Tukey's-b post hoc test to compare abundance estimates among riparian control, clearcut, and interior sites. The site served as the sample unit for these tests, with territory characteristics described as the mean value among each site's territories. The number of territories

with ≥ 50 song perches in a given site and year ranged from 1 to 6. The use of a site-based mean in statistical analysis was necessary to avoid pseudoreplication, since territory-holders on each site were related either by direct interaction or by common association with site-specific habitat characteristics (Hurlbert 1984). Previous Ovenbird researchers (Villard et al. 1993, Porneluzi et al. 1993, Donovan et al. 1995, King et al. 1996, Hagan et al. 1996, Sabine et al. 1996) have made the questionable assumption of independence among males sharing the same forest tract.

I performed a post hoc power analysis on each conventional test with GPOWER, a computer program designed for this purpose (Faul and Erdfelder 1992). In many comparisons, statistical power was low due to small effect and sample sizes. Below, I report results of conventional tests when their power was moderate to high (≥ 0.65, $\alpha = 0.1$), when their power was sufficient to detect a significant effect ($p < 0.1$), and when the effect size was below the level considered to be small ($d < 0.2$, $\alpha = 0.1$) (Cohen 1988). The conservative α level was selected in order to avoid Type II error, since erroneous conclusion of no treatment effect might harmfully misguide management efforts to protect riparian songbird communities.

Where the tests did not meet the power requirements, I employed randomization testing, a computer-intensive resampling approach that optimizes analysis of small data sets. I handled variables with one value per site (e.g. abundance) with the program RT 2.0 (Manly 1996). This program first calculated the observed mean difference (OMD) between two samples, next randomly re-assigned data points to the two categories 1000 times, and then generated a distribution of randomized mean differences (RMDs). If under 10% of the absolute RMDs equalled or exceeded the OMD, the result was considered significant ($p \leq 0.1$). I compared abundance data, pre- vs. post-harvest and treatment vs. control categories, in this manner. I also used RT 2.0 to compare the mean proportion of song perches occurring in given zones between riparian and clearcut sites.

I handled blocked data, where multiple dependent values were reported for each site (e.g. territory size), with Randcomp 0.1 (Brzustowski 1997). This program calculated a grand mean from the site means in a given category and defined the OMD as the difference between grand means. It then randomly re-assigned values to blocks and generated a distribution of randomized (grand) mean differences. As with RT 2.0, the proportion of absolute RMDs $\geq$ OMD represented the index of significance (p).

I used discriminant analysis (DA) to test for differences between the habitat structure of pre-harvest Ovenbird territories and that of habitat located 25m from the riparian forest edge. Since the distribution of basal area data did not meet the assumptions of DA, we analyzed this variable independently with a Mann-Whitney U test.

Due to lack of independence among neighboring males, the use of contingency tables in an analysis of pairing success was not possible without sacrificial pseudoreplication (Hurlbert 1984). Furthermore, the small number of individuals on each site resulted in crude, site-specific proportional measures. I therefore dismissed the option of mean comparisons and chose to report overall proportions of paired males.

In the text and tables that follow, results from randomization tests can be recognized by p-values unaccompanied by test statistics. All results derived from conventional methods, except for those appearing in graphs, report test statistics along with p-values.

2.3 **Results**

2.3.1 *Ovenbird Distribution Next to Lakes and Clearcuts*

There was an apparent effect of lake adjacency on Ovenbird abundance (Fig. 2.3). Fewer Ovenbirds occurred within 100m of lakes than in forest sites of similar dimensions that were situated (a) next to clearcuts and (b) within undisturbed upland stands. Despite low numbers close to the riparian edge, the number of Ovenbirds in the

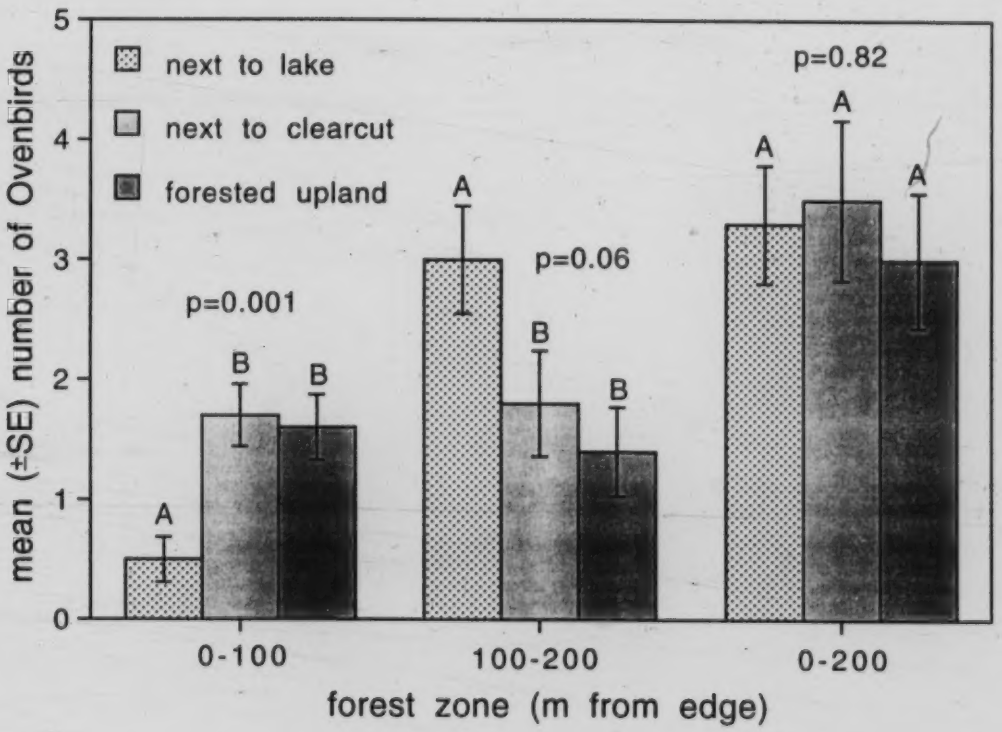


Figure 2.3. Mean number of Ovenbird territories in forest next to lakes (n=12 sites, 0-100m; n=6, 0-200m, and 100-200m), forests next to clearcuts (n=10), and in continuous upland forest tracts (n=10). Differences determined by one-way ANOVA. Column letters denote homogeneous groups identified by Tukey's-b post hoc test.

100-200m distance class exceeded that in clearcut and interior sites. Consequently, overall Ovenbird abundance in 200m-wide riparian tracts resembled estimates made in same-sized sites adjacent to clearcuts and in continuously forested uplands. Compared with interior sites, clearcut sites showed no effect of cutblock adjacency on Ovenbird abundance at either the 100m or 200m distances (Fig. 2.3).

Song perches were less likely to occur within the first 50m of both lakes and clearcuts than further away (Fig. 2.4). Here again, the influence of lake adjacency was stronger than that of clearcut adjacency, since the proportion of song perches occurring in zone 1 (within 50m of the edge) was significantly lower in riparian sites. For both site types, song perches were somewhat evenly distributed beyond 50m from the opening.

2.3.2 *Ovenbird Abundance in Buffer Strips*

None of the five 20m buffer strips contained Ovenbirds in 1997, the breeding season after harvest. Since Ovenbirds were rarely observed within 20m of lakes in intact riparian forests, this is not surprising. Ovenbirds were also absent from three buffer strips, surveyed in 1997 alone, ranging in width from 40m to 80m.

Extensive spot-mapping revealed no immediate post-harvest effect on Ovenbird abundance in 100m or 200m buffer strips (Table 2.2). Ovenbird numbers in undisturbed, riparian controls also remained stable between years. Intensive territory-mapping on a subset of sites verified the extensively gathered data, to a large extent mirroring magnitudes and non-significant changes. The one notable exception was on 100m control sites, where territory-mapping revealed a trend opposite that derived from spot-map estimates.

Randomization analysis of 1997 territory-map data showed no difference in abundance between seven 100m buffers ($x \pm SE = 1.31 \pm 0.45$) and six 100m controls (1.04 ± 0.35) ($p = 0.67$). Likewise, Ovenbird numbers in four 200m buffers (3.31 ± 0.34) did not differ significantly from six 200m controls (3.04 ± 0.51) ($p = 0.67$).

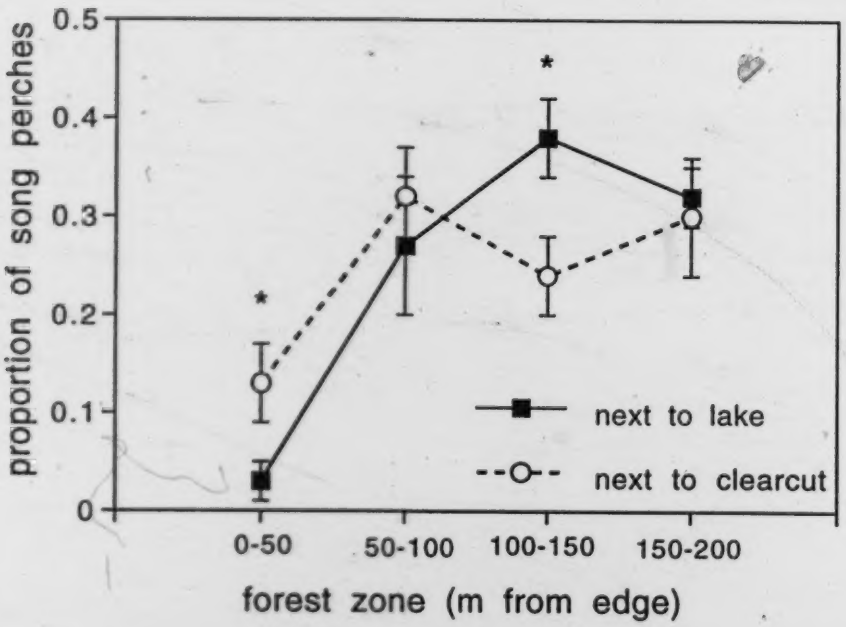


Figure 2.4. Mean proportion of Ovenbird song perches (± SE)in four designated zones at six sites next to lakes and seven sites next to clearcuts. * represents significant difference between lake and clearcut sites ($p<0.1$) as determined by Mann-Whitney U tests.

Table 2.2. Mean Ovenbird abundance before and after harvest in 100m and 200m buffer strips and in undisturbed control sites (SE in parentheses). Estimates were made by intensive territory-mapping on a subset of sites (TM), extensive spot-mapping on the same subset (SM), and extensive spot-mapping on all sites (SMA); n represents the number of sites in a given site class.

Method	Site Class	n	Before Harvest	After Harvest	Test	Test Statistic	p
TM	100m buffer	4	1.13 (0.26)	1.38 (0.31)	RT		0.54
SM	100m buffer	4	1.50 (0.56)	1.50 (0.43)	WSR*	Z=-0.447	0.66
SMA	100m buffer	6	1.40 (0.51)	1.60 (0.24)	WSR	Z=-0.447	0.66
TM	100m control	5	0.90 (0.17)	1.20 (0.38)	RT		0.48
SM	100m control	5	1.40 (0.22)	0.40 (0.22)	WSR	Z=-1.633	0.10
SMA	100m control	12	1.00 (0.21)	0.50 (0.19)	RT		0.11
TM	200m buffer	4	3.13 (0.41)	3.31 (0.34)	RT		0.74
SM	200m buffer†	4	3.00 (0.41)	3.00 (0.41)	WSR	Z=0.000	1.00
SMA	200m buffer†	6	2.50 (0.43)	2.50 (0.43)	WSR	Z=0.000	1.00
TM	200m control	5	3.45 (0.47)	3.30 (0.54)	WSR	Z=-0.271	0.79
SM	200m control†	5	3.00 (0.71)	2.80 (0.37)	WSR	Z=-0.447	0.66
SMA	200m control†	12	2.33 (0.38)	2.25 (0.28)	RT		0.87

*Wilcoxon signed-ranks test

†Upland limit of mapping was 150m from lake-side forest edge.

2.3.3 *Territory Dimensions*

Mean territory size decreased in 100m and 200m buffers after harvest and increased in their respective controls. However, none of the changes were statistically significant (Table 2.3).

In general, territory shapes ranged widely from compact to elongated (Forman 1995), before and after harvest (Appendix 5). The index of circularity registered no significant difference between years in any site class. Nonetheless, there was evidence of territory compression in buffer strips. In both 100m and 200m buffers the mean length of minor territory axes decreased by about 30m, compared to a decrease of < 5m in their respective control groups. This response was significant in 200m strips, but not in the 100m buffers. Major axis lengths were highly variable in all classes with no significant differences detected (Table 2.3).

2.3.4 *Territory Position*

Upland harvest caused a down-slope shift in Ovenbird territory position within 100m buffer strips (Table 2.4, Fig. 2.5). The mean minimum distance from territory boundary to riparian forest edge decreased significantly from 16.54m before harvest to 6.33m after harvest. A comparison of six 100m buffers and six control sites in 1997 showed a more dramatic contrast. In unharvested areas territories were positioned, on average, 48.25m (SE = 5.33) from the riparian edge, whereas the upland distance of Ovenbird territories in 100m buffers was 12.08m (SE = 5.94). The four-fold difference was highly significant (U = 0.00, p = 0.001).

In the four 100m buffers that were mapped intensively each year, territory shifts more than doubled the mean proportion of Ovenbird territory area occurring in zone 1, the lake-side 50m (Fig. 6). Randomization tests showed the effect was significant (p = 0.05). Once again, the contrast was more pronounced between 1997 harvest and control sites. In six 100m buffers, the average proportion of Ovenbird territory area occurring in zone 1 was 0.37 (SE = 0.09). This value exceeded, by over six times, the

Table 2.3. Effect of upland harvest on Ovenbird territory size and shape. Mean values are reported with SE in parentheses; n represents the number of sites in a given site class.

Variable	Site Class	n	Before Harvest	After Harvest	Test	Test Statistic	p
Territory size (ha)	100m buffer	4*	1.76 (0.29)	1.45 (0.33)	RC†		0.53
	100m control	5	1.36 (0.10)	1.68 (0.33)	WSR††	Z=-0.944	0.35
	200m buffer	4	1.60 (0.26)	1.36 (0.06)	RC		0.50
	200m control	5	1.34 (0.11)	1.65 (0.32)	RC		0.57
Circularity+	100m buffer	4	1.42 (0.09)	1.46 (0.10)	RC		0.80
	100m control	5	1.43 (0.03)	1.51 (0.08)	RC		0.67
	200m buffer	4	1.43 (0.05)	1.37 (0.03)	RC		0.48
	200m control	5	1.41 (0.03)	1.53 (0.08)	WSR	Z=-0.944	0.35
Length of minor axis (m)	100m buffer	4	108.25 (15.22)	76.67 (12.20)	RC		0.24
	100m control	5	111.00 (8.80)	106.60 (5.78)	RC		0.72
	200m buffer	4	125.25 (11.40)	97.25 (6.80)	WSR	Z=-1.826	0.07
	200m control	5	108.00 (8.27)	106.40 (4.97)	RC		0.89
Length of major axis (m)	100m buffer	4	229.00 (19.94)	251.00 (41.51)	RC		0.64
	100m control	5	177.40 (7.47)	241.40 (55.59)	RC		0.37
	200m buffer	4	188.25 (21.15)	192.50 (10.31)	WSR	Z=-0.365	0.72
	200m control	5	179.00 (6.46)	240.60 (55.73)	RC		0.37

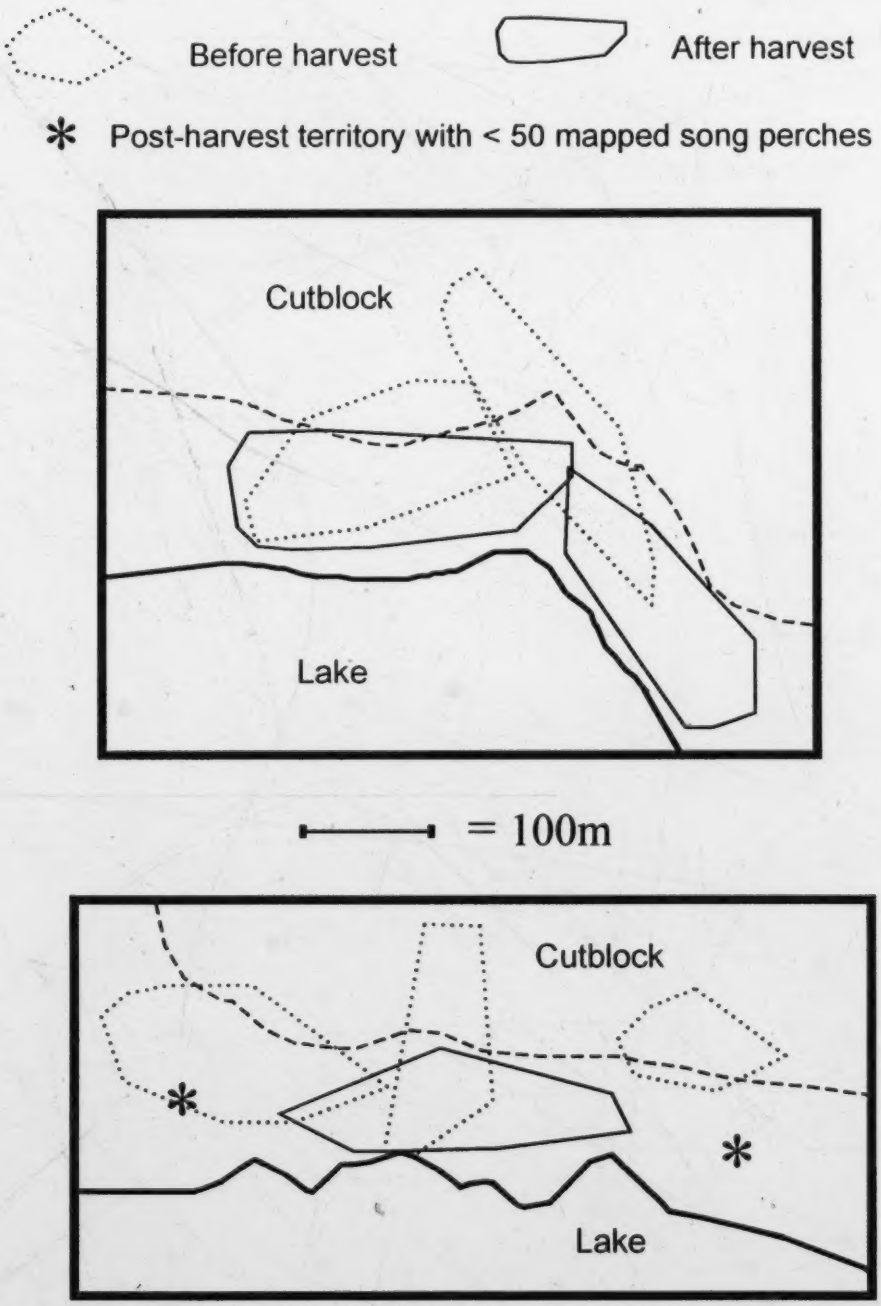
* no birds at one 100m buffer post-harvest
† Randcomp
†† Wilcoxon signed-ranks test
+ $(0.282)(\text{perimeter})/(\text{area})^{1/2}$ = 1.0 for a circle, 1.12 for a square, and infinity for an infinitely long and narrow shape

Table 2.4. Effect of upland harvest on Ovenbird territory position. Values are reported as means (with SE in parentheses) and represent minimum distance from territory boundary to riparian forest edge; n represents the number of sites in given site class.

Variable	Site Class	n	Before Harvest	After Harvest	Test	Test Statistic	p
Distance to edge (m)	100m buffer	4*	16.54 (5.99)	6.33 (5.36)	WSR'	Z=-1.604	0.05
	100m control	5	31.53 (4.73)	40.36 (6.54)	RC''		0.58
	200m buffer	4	45.58 (10.40)	41.75 (10.93)	WSR	Z=-0.365	0.72
	200m control	5	47.97 (8.83)	54.65 (6.26)	RC		0.59

* no birds at one 100m buffer post-harvest
' Wilcoxon signed-ranks test
'' Randcomp

Figure 2.5. Pre- and post-harvest position of Ovenbird territories in two 100m buffers.



proportion recorded in control sites (0.06 ± 0.03) (U = 4.0, p = 0.01). The average area of zone 1 occupation per bird reflected the difference in proportions: 0.49 ± 0.14ha in 100m buffers vs. 0.11 ± 0.07 ha in 100m controls (U = 5.0, p = 0.02). The proportion of zone 2 occupancy (50 to 100m from riparian edge) did not change as a result of upland harvest (Fig. 2.6).

In 200m buffer strips, the mean minimum distance from territory boundary to riparian edge did not change after harvest (Table 2.4). Figure 2.6 shows a slight, non-significant increase in the proportion of Ovenbird territory area occurring in zones 1 and 2. Figure 2.7 reinforces this suggestion of positional change, demonstrating a significant difference in Ovenbird distribution within 200m buffer strips compared to contemporary controls. In 200m buffers, the area within 100m of the riparian edge contained about three times more Ovenbirds than the same zone in undisturbed riparian sites. The adjacent 100m, consisting of zones 3 and 4, contained half as many Ovenbirds as the same area in control forests. In both cases, differences were significant ($p < 0.1$).

2.3.5 *Vegetation Structure*

As previously detailed, a lakeward shift in territory position occurred in 100m buffers and to a lesser extent in 200m buffers. The change in territory placement could have resulted in changes to major structural attributes of Ovenbird territories. However, for six variables (canopy cover, tree height, shrub cover, shrub height, herb cover, litter depth), discriminant analysis did not distinguish between 36 vegetation plots situated in zone 1 (25m from the riparian forest edge) and the 36 plots located in zones 2-4, within pre-harvest Ovenbird territories (Wilks' Lambda = 0.906, p = 0.36). For a seventh variable, tree basal area, a Mann-Whitney U-test also failed to show a difference (U = 558.0, p = 0.31) (see Table 2.5 for mean values).

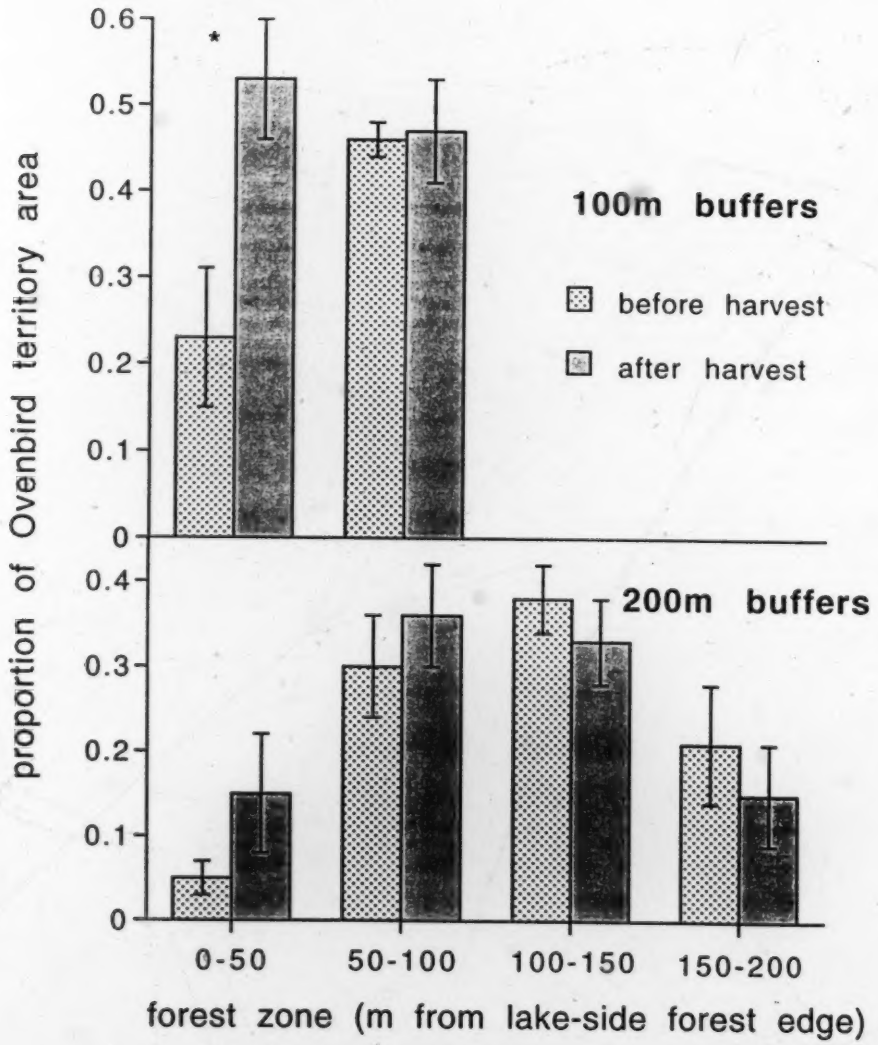


Figure 2.6. Mean proportion of Ovenbird territory area (± SE) in designated zones within 100m (n=4 before harvest, n=3 after harvest) and 200m buffer strips (n=4). * represents p=0.05 as determined by a one-tailed Wilcoxon signed-ranks test.

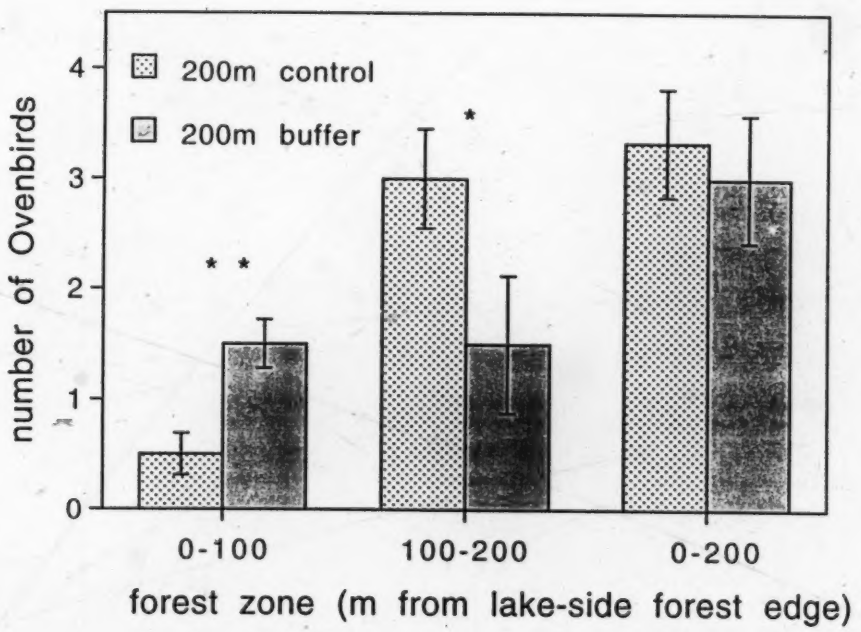


Figure 2.7. Mean number of Ovenbirds (± SE) in three riparian forest zones in 1997. Compared are undisturbed control sites (n=12, 0-100m; n=6, 100-200m and 0-200m) and 200m buffer strips (n=6). Estimates are based on extensive spot-mapping. * represents $p<0.1$ and ** represents $p=0.01$ as determined by Mann-Whitney U tests.

Table 2.5. Structural characteristics of zone 1 habitat vs. Ovenbird territories. Values represent means with SE in parentheses.

Variable	Zone 1 (n=36)	Ovenbird territory (n=36)
canopy cover	0.74 (0.02)	0.78 (0.02)
canopy height (m)	20.67 (0.66)	21.29 (0.62)
shrub cover	0.23 (0.03)	0.16 (0.02)
shrub height (cm)	89.72 (6.61)	82.64 (4.64)
herb cover	0.23 (0.02)	0.27 (0.02)
litter depth	68.56 (5.73)	69.44 (5.35)
tree basal area ($cm^2/100m^2$)	3337.15 (331.86)	3506.76 (181.96)

2.3.6 *Pairing Success*

Male pairing success in 100m and 200m buffer strips was affected by upland harvest in opposite directions (Table 2.6). The 100m group had a higher percentage of paired males after treatment than before, 100% up from 71%. Meanwhile, pairing success in the 200m group decreased from 100% to 73%. Pairing levels did not differ notably between years at the control sites. When figures from 100m, 200m, and control sites were combined, the overall proportion of mated males was the same after harvest (83%) as before (84%). The post-harvest addition of three 100m buffer strips and one control site did not influence estimates of pairing success.

Table 2.6. Percentage of male Ovenbirds paired before harvest, after harvest on the same sites, and after harvest with sites added.

Site Class	Before Harvest	After Harvest	After with Added Sites
100m buffer*	71% (7)†	100% (7)	100% (14)
200m buffer	100% (10)	73% (11)	73% (11)
nested control††	79% (14)	83% (18)	82% (22)
overall	84% (31)	83% (36)	85% (47)

* Three additional 100m buffer strips were sampled after harvest.
† (n) = total number of designated individuals combined from all sites in a given class
†† One additional control site was sampled after harvest

2.4 **Discussion**

2.4.1 *Ovenbird Distribution Next to Lakes and Clearcuts*

The pattern of Ovenbird distribution near lakes and clearcuts shows the relative importance of the two edge types that bound buffer strips. The negative influence of lake adjacency on the use of zones 1 and 2 (Figs. 2.3-2.5) reflects the Ovenbird's association with upland forest. Studies conducted throughout its range confirm the pattern observed here: greater abundance in uplands compared to riparian habitat (Wenny et al. 1993, LaRue et al. 1995, Hawrot and Niemi 1996).

The concentration of brood parasitic Brown-headed Cowbirds (*Molothrus ater*) at the land-water interface (Gates and Giffen 1991, Machtans 1996) may partially explain this phenomenon. Niche separation between the Ovenbird and other members of its guild may also underlie the results. While wintering in Central America, Ovenbirds occupy dry sites up-slope of congenerics, the waterthrushes (Lack and Lack 1972). Ground-foraging and ground-nesting species in Missouri separate along a local topographic gradient as well, with Ovenbirds occurring at the highest, moderately sloped elevations (Wenny et al. 1993). The Northern Waterthrush (*Seiurus noveboracensus*), the most closely related species in the boreal forest, was uncommon on the sites under investigation (unpubl. data). A third possibility is that resources situated close to the lake edge (e.g. prey, nesting sites, song perches) do not satisfy the

Ovenbird's breeding requirements. It is not clear whether these factors operate individually or in combination to deter Ovenbird use of lake-side habitat in Alberta. However, the proposition of a psychological aversion to edges in general (MacClintock et al. 1977) can be rejected since Ovenbird distribution was not influenced by clearcut edges in the same system.

Within 100m of clearcuts, Ovenbird numbers were comparable to those observed in forest interiors (Fig. 2.3). The lack of a clearcut edge effect on Ovenbird abundance is in accordance with other research conducted in silvicultural settings (Thompson et al. 1992, Welsh and Healy 1993, Sabine et al. 1996, Yahner 1997, King et al. 1996, 1997). The relatively low use of zone 1 (Fig. 2.4) seems to be a function of geometry, whereby the concentration of song perches at the center of polygonal territories favors detection away from a habitat boundary (Kroodsma 1982, King et al. 1997). The boundary effect was not strong enough to cause differences between clearcut edge and interior abundance estimates. This may be due, in part, to effects of mapping resolution and scale. In the future, researchers should create detailed territory maps next to clearcuts and in interior forests to more narrowly define a distance threshold for the clearcut boundary effect.

In both clearcut and riparian sites, the number of song perches increased with distance from the edge, reached a peak, and then declined. The peaks may have coincided with song centers located at the core of Ovenbird territories (Zach and Falls 1978). Offset peaks, caused by differential edge effects, resulted in dissimilar use of zone 3.

The mounting evidence from managed forests contradicts reports of Ovenbird edge avoidance in agricultural woodlots (MacClintock et al. 1977, Wenny et al. 1993). Therefore, it is important to distinguish between farming and forestry in predicting management effects. Likewise, lake and clearcut edges warrant distinction, the former more strongly influencing Ovenbird distribution than the latter. Indeed, the aquatic-

terrestrial ecotone more closely resembles the field-forest ecotone in its influence on Ovenbird numbers. Both are maintained, multi-layered transition areas which lack the abrupt structure and ephemeral quality of clearcut edges.

As clearcut edges age, they may assume structural attributes, characteristic of agricultural and riparian edges, that diminish Ovenbird habitat suitability (e.g. high shrub density). If such an edge effect were to penetrate well into a forest, Ovenbird territories may shift to the interior. In time, as growth in the cutblock softens the edge, territories would be expected to shift back and eventually overlap the boundary. Effects of edge age on songbird distribution is a promising avenue for future research.

2.4.2 *Ovenbird Abundance in Buffer Strips*

The predicted absence of Ovenbirds from 20m buffer strips confirms previous work performed in narrow riparian reserves (Stauffer and Best 1980, Triquet et al. 1990). It is also consistent with repeated studies showing exceptionally low abundance in small forest patches (e.g. Gibbs and Faaborg 1990, Villard et al. 1993). Ovenbird territories, normally exceeding 100m across at their most narrow point (Table 2.3), will not conform to the suitably structured habitat available in 20m buffers. Widths of 40-80m also appear to be insufficient.

In widths of 100m, however, Ovenbird numbers were conserved, at least in the short term. The persistence of Ovenbirds in 100m buffers, at pre-harvest levels, does not support my prediction. It also contradicts the results of Machtans (1996), who worked in the same ecoregion. He found that upland clearcutting reduced the number of Ovenbirds in 100m lakeshore buffer strips. The contrasting results may indicate a critical threshold at 100m.

As predicted, 200m buffer strips supported Ovenbird populations at pre-harvest levels. Post-harvest crowding did not occur in this or any other buffer width as it has among other species in buffers (Darveau et al. 1995) and among Ovenbirds in isolated fragments (Hagan et al. 1996). Lack of a density increase suggests that remnant forest,

averaging over 80% of the land area within 800m of lakes, absorbed individuals displaced from disturbed areas. Unchanging density reduced the likelihood that territory characteristics, such as size and shape, would respond to treatment.

2.4.3 *Territory Dimensions*

Territory size changes, described by decreases in 100m and 200m buffers concurrent with increases in their respective controls, were not statistically significant (Table 3). Without information on resource availability, it is difficult to assess this pattern's biological significance. According to Huxley's (1934) elastic disk model, territories are compressable up to a point beyond which resources become limiting. It is unlikely that a critical point was reached in this experiment for two reasons. First, the natural variability in territory size was great in both treatments and controls (Table 2.3). Second, buffer strip territories measured well within the range of sizes observed elsewhere: 0.20-1.80ha in Michigan (Hann 1937), 0.61-1.60ha in Ontario, and 0.88-1.40ha in Missouri (Wenny 1989). Nonetheless, geographic variability in territory size, associated with differences in vegetation structure and invertebrate abundance (Stenger and Falls 1959), limits the authority of such inter-regional comparisons (Wiens et al. 1985).

The territory shape data are also ambiguous. Although the circularity index shows no effect of harvest in either width, territories in 200m buffers narrowed (Table 2.3). Had narrowing been consistently accompanied by elongation, the fitness of territory holders may have been reduced. Increased time and energy expenditure in territory defense might have limited pair-bonding, mate-guarding, and feeding opportunities (Verner 1977). Since major territory axes did not show a consistent response, I recognize no negative effects of territory narrowing in 200m buffers. The narrowing observed in some 100m buffers is even less likely to have impaired territory-holders. Because their territory boundaries largely conformed to "hard-edged" buffer strip

boundaries (Appendix 5), males occupying 100m buffers most likely experienced low intruder pressure (Stamps et al. 1987).

Still, clearcut edges were not entirely impermeable. Of the 11 males occupying 100m buffer strips, 2 were observed crossing clearcut boundaries. One occasionally sang in the adjacent cutblock from two residual tree clumps located 15m and 65m from the clearcut edge. The clumps measured approximately 0.02ha and 0.1ha respectively. Another male, whose territory included a leave area contiguous with the buffer strip, crossed the cutblock corner in a two-stage flight over approximately 150m. In this case, a residual tree clump served as a "stepping stone."

2.4.4 *Territory Position*

A pre- and post-harvest abundance comparison in 200m buffers demonstrates increased use of zones 1 and 2 after treatment. However, detailed territory maps show the changes in position were minor. By contrast, territories in 100m buffers shifted significantly lakeward. Considering the dimensions of Ovenbird territories, this result was predictable in the absence of gross territory compression or distortion. A sharp increase in the use of zone 1 would be unimportant if it did not result in increased vulnerability to the local predator/parasite complex, elevated interspecific competition, or changes in prey availability - variables beyond the scope of this project. However, if relocated territories contain atypical vegetation structure, they may be rejected by females using structural cues to evaluate territory quality (Smith and Shugart 1987).

We found no structural differences between vegetation plots situated 25m from the riparian forest edge and those located in pre-harvest Ovenbird territories. More intensive vegetation analysis in the same area suggests that the influence of the riparian edge on canopy cover and shrub cover penetrates no more than 5m. However, sapling density is exceptionally high up to 20m from the edge and the mid-canopy layer is more fully developed in the 0-40m zone than further upland (K. Harper pers. comm.). This pattern corresponds with the Ovenbird's pre-harvest absence from zone 1. Elsewhere

in Alberta, Ovenbirds are least abundant where shrubs and saplings are dense and the canopy is low (Westworth and Telfer 1993, Schieck and Nietfeld 1995). Although relocated territories may have differed in these structural characteristics, females were not deterred from selecting mates in 100m buffers.

2.4.5 *Pairing Success*

The increase in pairing success in 100m buffers, from 71% to 100%, and the opposite pattern in 200m strips (100% to 73%) seem counterintuitive. However, the figures were derived from relatively small sample sizes ($7 < n < 14$). In addition, they fell symmetrically outside the range reported for normally paired Ovenbirds in northern hardwood forests, 80% (Hagan et al. 1996) to 91% (King et al. 1996). When sites were pooled in each year to increase sample sizes, the overall proportion of paired males remained constant (Table 2.6), at the mid-point of the published range. Therefore, I conclude that differences resulted from chance and small sample sizes and that clearcutting did not influence pairing success in 100m or 200m buffer strips.

This conclusion is consistent with other studies showing no effect of timber activity on Ovenbird abundance or pairing success in remnant forests (Sabine et al. 1996, King et al. 1996). However, it contradicts the observation of low pairing success associated with short-term density increases in isolated silvicultural fragments (Hagan et al. 1996). By preventing crowding, the availability and connectivity of unharvested forest seem to ameliorate short-term disturbance effects on pairing success. High regional forest cover also reduces edge effects on abundance of Ovenbirds (Robbins et al. 1989, Porneluzi et al. 1993), brood parasitism (Robinson et al. 1995, Donovan et al. 1995), and nest predation (Andren 1995).

Research in agricultural mosaics has demonstrated low Ovenbird pairing success in edge-dominated habitat (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). In this study, the lack of a disturbance effect on pairing in 100m buffers reinforces the distinction between agricultural and silvicultural influences

on songbirds. Cotterill (1996) and Song (pers. comm.) first noted this distinction in Alberta's boreal mixed-wood forest in studies of artificial nest predation and bird community composition. As in this study, neither researcher detected clearcut edge effects.

The most evident effects of timber activity on Ovenbirds in Alberta will result directly from habitat alteration. After harvesting, Ovenbirds will disappear from cutblocks for at least 14 years (Westworth and Telfer 1993). Eventually, Ovenbirds are expected to recolonize these areas and reach peak densities between 30 and 65 years after disturbance (Westworth and Telfer 1993, Schieck and Nietfeld 1995). If cutblocks age beyond the anticipated rotation time (60-70 years), canopy breaks and increased shrub development may reduce their suitability to Ovenbirds (Quinlan et al. 1990, Westworth and Telfer 1993, Schieck and Nietfeld 1995). In fact, by replacing forests at the age-class extremes with stands of intermediate age, timber activity may gradually favor Ovenbirds.

Predicted harvest effects vary by temporal and spatial scale. Whereas short-term effects may be negative at the stand level, long-term effects may be positive at the landscape level. Ultimately, the persistence of Ovenbirds within a managed area depends on the availability and connectivity of mature upland forest. Therefore, rotation lengths, pass intervals, and corridor protection are more important issues for regional Ovenbird conservation than buffer strip width. Nonetheless, because buffer strips facilitate Ovenbird dispersal (Machtans et al. 1996) and reduce songbird turnover in connected forest patches (Schmiegelow et al. 1997), these riparian corridors may figure prominently in a regional conservation strategy. Efforts to retain buffer strips as corridors should recognize that their value increases with width (Saunders et al. 1991).

2.4.6 *Conclusions*

These findings provide a basis for buffer strip management that will protect songbird communities. In extensively wooded landscapes, a 100m forested buffer

seems adequate to conserve Ovenbird numbers in the short term. This width does not include lakeshore, wetland, or shrub zones. Though most likely unsuitable for Ovenbirds, buffers of lesser width may conserve species that tolerate riparian and clearcut edges and/or have smaller territories than Ovenbirds. However, forest species with larger territories (e.g. tanagers and grosbeaks) may require wider riparian forest reserves. For Ovenbirds, maintenance of 200m buffers would avoid potential, unforeseen effects of a lakeward shift in territory position. Moreover, since wide corridors promote more wildlife movement than narrow corridors (Saunders et al. 1991), 200m buffers may more effectively channel dispersing Ovenbirds than 100m buffers. By promoting vital genetic exchange and resettlement of depleted patches, wide buffer strips would ameliorate the short-term, local effects of habitat loss.

This study has expanded the understanding of silvicultural effects on the value of riparian habitat. The new approach, using a combination of abundance, pairing and detailed territory data, warrants repetition in the boreal mixed-wood forest and in other ecosystems. Ideally, efforts to repeat it will include further examination of territory dimensions and intruder pressure, direct measures of productivity, and an invertebrate sampling protocol. These indices would more sensitively measure the quality of buffer strip habitat.

Finally, the limitation of short-term data sets must be emphasized. Because the immediate response of a buffer strip bird community to upland harvest may differ from its long-term response (Darveau et al. 1995), future studies should involve multiple breeding seasons and/or a chronosequence. Nonetheless, short-term measurements provide researchers and foresters a basis for predicting long-term management impacts.

2.5 Literature Cited

Alberta Environmental Protection. 1996. The Status of Alberta's Timber Supply. Edmonton, AB.

Alberta-Pacific Forest Industries, Inc. 1993. Timber Harvest Planning and Operating Ground Rules, Boyle, AB.

Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pp. 225-255 *in* L. Hansson, L. Fahrig, and G. Merriam (eds.), Mosaic Landscapes and Ecological Processes, Chapman and Hall, London.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird Census Techniques. Academic Press, Toronto, ON.

Bormann, F. H., and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, NY.

Brode, J. M., and R. B. Bury. 1984. The importance of riparian systems to amphibians and reptiles. Pp. 30-36 *in* R. E. Warner and K. M. Hendrix (eds.), California Riparian Ecosystems: Ecology, Conservation and Productive Management, University of California Press, Berkeley.

Brzustowski, J. 1997. Randcomp 0.1 (computer program). University of Alberta Department of Biological Sciences, Edmonton, AB.

Budd, W. W., P. L. Cohen, P. R. Saunders, and F. R. Steiner. 1987. Stream corridor management in the Pacific Northwest: I. Determination of stream-corridor widths. Environmental Management 11:587-597.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest.

Chapman, L., L. B. Miller, and D. J. McQueen. 1996. Riparian zones as corridor, habitat and buffer: a preliminary literature review. York University, Toronoto.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences, 2nd edition. L. Erlbaum Associates, Hillsdale, NJ.

Cotterill, S. E. 1996. Effect of clearcutting on artificial egg predation in boreal mixedwood forests in north-central Alberta. M.S. thesis, University of Alberta, Edmonton.

Darveau, M., P. Beauchesne, L. Belanger, J. Huot, and P. LaRue. 1995. Riparian forest strips as habitat for breeding birds in the boreal forest. Journal of Wildlife Management 59:67-78.

Donovan, T. M., F. R. Thompson, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380-1395.

Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy 71:14-23.

Faul, F., and E. Erdfelder. 1992. GPOWER: A priori, post-hoc, and compromise power analyses for MS-DOS (computer program). Bonn University Department of Psychology, Bonn, FRG.

Forman, R. T. T. 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge, UK.

Gates, J. E., and N. R. Giffen. 1991. Neotropical migrant birds and edge effects at a forest-stream ecotone. Wilson Bulletin 103:204-217.

Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conservation Biology 2:193-196.

Gibbs, J. P., and D. G. Wenny. 1993. Song output as a population estimator: effect of male pairing status. Journal of Field Ornithology 64:316-322.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective on riparian zones. Bioscience 41:54-551.

Hagan, J. M., III, W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188-202.

Hann, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bulletin 49:145-237.

Hawrot, R. Y., and G. J. Niemi. 1996. Effects of edge type and patch shape on avian communities in a mixed conifer-hardwood forest. Auk 113:586-598.

Hornbeck, J. W., C. W. Martin, and C. T. Smith. 1986. Protecting forest streams during whole tree harvesting. Northern Journal of Applied Forestry 3:97-100.

Hurlbert, S. H. 1984. Pseudo-replication and the design of field experiments. Ecological Monographs 54:187-211.

Huxley, J. S. 1934. A natural experiment on the territorial instinct. British Birds 27:270-277.

Johnson, E. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. Endangered habitats: a concept. Pp. 68-80 in R. R. Johnson and D. A. Jones (eds.), Importance, Preservation, and Management of Riparian Habitat: A Symposium. US Forest Service, Fort Collins, CO.

Johnson, W. N., and P. W. Brown. 1990. Avian use of a lakeshore buffer strip and an undisturbed lakeshore in Maine. Northern Journal of Applied Forestry 7:114-117.

King, D. I., C. R. Griffith, and R. M. DeGraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in a forested landscape. Conservation Biology 101:1380-1386.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. Wilson Bulletin 109:239-245.

Krebs, J. R. 1971. Territory and breeding density in the great tit, Parus major L. Ecology 52:2-22.

Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. Journal of Applied Ecology 19:361-370.

Lack, D., and P. Lack. 1972. Wintering warblers in Jamaica. Living Bird 11:129-153.

LaRue, P., L. Belanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. Canadian Journal of Forest Research 25:555-566.

Lein, M. R. 1980. Display behavior of Ovenbirds. I. Non-song vocalizations. Wilson Bulletin 92:312-329.

Lein, M. R. 1981. Display behavior of Ovenbirds (*Seiurus aurocapillus*): II. Non-song vocalizations. Wilson Bulletin 93:21-41.

MacClintock, L., R. F. Whitcomb, and B. L. Whitcomb. 1977. Island biogeography and habitat islands of eastern forest. II. Evidence for the value of corridors and minimization of isolation in the preservation of biotic diversity. American Birds 31:6-12

Machtans, C. S. 1996. Riparian buffer strips: their value as habitat and movement corridors for songbirds in the boreal mixedwood forest of Alberta. M.S. thesis, University of Alberta, Edmonton.

Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology 10:1366-1379.

Manly, B. F. J. 1996. RT 2.0: A program for randomization testing (computer program). The Centre for Applications of Statistics and Mathematics, University of Otago, Dunedin, NZ.

Martin, C. W., and R. S. Pierce. 1980. Clearcutting patterns affect nitrate and calcium in New Hampshire streams. Journal of forestry 778:268-272.

McGarigal, K., and N. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. Journal of Wildlife Management 56:10-23.

Mills, G. S., J. B. Dunning, and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. Wilson Bulletin 103:468-482.

Morse, D. H. 1976. Variables affecting the density and territory size of beeding spruce woods warblers. Ecology 57:290-301.

Porneluzi, P., J. C. Bednarz, L. J. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. Conservation Biology 7: 618-622.

Quinlan, R. W., W. A. Hunt, K. Wilson, J. Kerr. 1990. Habitat requirements of selected wildlife species in the weldwood forest management agreement area. Alberta Environmental Protection, Edmonton, AB.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103: 1-34.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 167:1987-1990.

Sabine, D. L., A. H. Boer, and W. B. Ballard. 1996. Impacts of habitat fragmentation on pairing success of male Ovenbirds, Seiurus aurocapillus, in Southern New Brunswick. The Canadian Field-Naturalist 110:688-693.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Schieck, J., and M. Nietfeld. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. Pp. 115-157 *in* J. B. Stelfox (ed.), Relationships Between Stand Age, Stand Structure and Biodiversity in Aspen Mixedwood Forests in Alberta. Jointly published by Alberta Environmental Centre, Vegreville, AB, and Canadian Forest Service, Edmonton, AB.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914-1932.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.

Semenchuk, G. P. 1992. The Atlas of Breeding Birds of Alberta. Federation of Alberta Naturalists. Edmonton

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68:695-704.

Spackman, S. C., and J. W. Hughes. 1995. Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. Biological Conservation 71:325-332.

Stamps, J. A., M. Buchner, and V. V. Krishnan. 1987. American Zoologist 27:307-325.

Stauffer, D. F., and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. Journal of Wildlife Management 44:1-15.

Stenger, J., and J. B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bulletin 71:125-140.

Thompson, F. R., III, W. D. Dijak, T. G. Kulowiec, and D. A. Hamilton. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. Journal of Wildlife Management 56:23-30.

Triquet, A. M., G. A. McPeek, and W. C. McComb. 1990. Songbird diversity in clearcuts with and without a riparian buffer strip. Journal of Soil and Water Conservation 45:500-503.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). No. 88 in A. Poole and F. Gill (eds.), Birds of North America. The Academy of Natural Science of Philadelphia, PA.

Van Horn, M. A., R. M. Gentry, and J. Faaborg. 1995. Patterns of Ovenbird (Seiurus aurocapillus) pairing success in Missouri forest tracts. Auk 112:98-106.

Van Horne, B. 1983. Density is a misleading indicator of habitat quality. Journal Wildlife Management 47:893-901.

Verner, J. 1977. On the adaptive significance of territoriality. American Naturalist 111:769-775.

Vickery, P. D., M. L. Hunter, and J. V. Wells. 1992. Is density an indicator of breeding success? Auk 109:706-710.

Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (Seiurus aurocapillus). Auk 110:759-768.

Wander, S. A. 1985. Comparative breeding biology of the Ovenbird in large vs. fragmented forests: implications for the conservation of neotropical migrant birds. Ph.D. dissertation, Rutgers University, New Brunswick, NJ.

Welsh, C. J. E., and W. M. Healy. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. Wildlife Society Bulletin 21:143-154.

Wenny, D. 1989. Population density and area requirements of three forest interior warblers in central Missouri. M.A. thesis, University of Missouri, Columbia.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection, and minimum area requirements of three forest interior warblers in central Missouri. Condor 95:968-979.

Westworth, D. A., and E. S. Telfer. 1993. Summer and winter bird populations associated with five age-classes of aspen forest in Alberta. Canadian Journal of Forest Research 23:1830-1836.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1985. Territory size variations in shrubsteppe birds. Auk 102:500-505.

Yahner, R. H. 1997. Long-term dynamics of bird communities in a managed forest landscape. Wilson Bulletin 109:595-613.

Zach, R., and J. B. Falls. 1978. Bivariate normal song territories in ovenbirds. Canadian Journal of Zoology 56:2088-2092.

Chapter Three

Songbirds in Riparian Buffer Strips of the Boreal Mixed-wood Forest: Analysis of Management Options and Research Needs

3.1 Summary of Findings

The previous chapter detailed the short-term response of Ovenbirds to upland timber harvest in buffer strips of various widths. These area-sensitive songbirds did not occur in buffer strips whose forested areas measured ≤ 80m across. Contrary to previous results from the boreal mixed-wood forest, 100m buffers supported Ovenbirds at pre-harvest abundance levels. A lakeward shift in territory position enabled continued occupation of the riparian forest. Coarse-scale data showed that the shrub and canopy layers of the newly settled zone did not differ from upland habitat. Related research, performed at a fine scale on a subset of Ovenbird study sites, found sapling density and mid-canopy cover to be higher within 20m and 40m of lakes, respectively. However, this structural difference did not influence the ability of males to attract mates. The creation of 200m buffer strips influenced Ovenbirds to an even smaller degree. As in 100m buffers, abundance and pairing success were unaffected by upland clearcutting. Territories narrowed and shifted slightly lakeward following treatment, but did not contain significantly higher proportions of riparian edge habitat.

Brown-headed Cowbird, Raven (*Corvus corax*), and red squirrel (*Tamiasciurus hudsonicus*) sightings increased significantly after harvest in 100m buffer strips, while Cowbirds and Ravens also increased in 200m buffers (Appendix 2). Because olfactory predators are better equipped than visual predators to detect well-concealed ground nests, the red squirrel may pose the most serious predatory threat to Ovenbird nest success. Therefore, predation risk could be higher in 100m buffers than in 200m strips as long as elevated red squirrel numbers persist. Overall, the sensitivity of breeding Ovenbirds to upland clearcutting decreased with increasing buffer width.

3.2 **Potential Functions of Buffer Strips**

Foresters and wildlife biologists must integrate upland and riparian management to achieve landscape-level objectives. In an integrated harvest plan, buffer strips could perform numerous roles in the interest of songbird conservation. Advisable, minimum width standards will vary according to the defined role. Without clear objectives for buffer strip function, riparian forest management will continue to influence songbird populations in a haphazard manner. Below, I discuss four possible functions of buffer strips in terms of avian conservation. Each is placed in context of the emerging understanding of Ovenbird breeding biology.

First, strips of riparian forest can act as movement corridors for natal dispersal (Machtans et al. 1996) and migration (Emmerich and Vohs 1982). In Alberta's boreal forest, juvenile Ovenbirds readily dispersed through 100m buffer strips, but avoided crossing clearcuts (Machtans et al. 1996). Dispersal through buffers reduced species turnover in connected forest patches (Schmiegelow et al. 1997). By facilitating gene flow, buffer-corridors may also minimize the risk of local extinction posed by inbreeding depression. Although little is known about bird movement through corridors of various widths, wide corridors generally facilitate more wildlife movement than narrow ones (Saunders et al. 1991). Continuing research in 100m buffers in the boreal mixed-wood forest will further define their value as channels for dispersal.

The second possible role of a riparian buffer strip is to conserve songbird species concentrated in, or uniquely associated with riparian forests. Machtans (1996) found 26% more species and 25% more individuals at lake-side point count stations than at upland stations. Six species were more abundant near the lake (Lincoln's Sparrow, Song Sparrow, Brown-headed Cowbird, Western Tanager, Yellow Warbler) and two occurred there exclusively (Alder Flycatcher, Red-winged Blackbird). It is possible that the minimum forested buffer required to retain these lake-associated species is less than that necessary to conserve the Ovenbird, which is negatively associated with

riparian edges. Data from the TROLS community-level bird study will address this possibility.

A third potential function of buffer strips in a songbird management strategy is to provide refuge for species dependent on old-growth forests. After two to three passes through aspen-dominated uplands, old forests may be concentrated in riparian reserves. Due to fire suppression in managed areas and naturally low fire frequency in riparian zones (Suffling et al. 1982, but see Burgess 1997), buffer strips could ultimately favor species associated with old-growth (e.g. Black-throated Green Warblers, Brown Creepers).

Ovenbirds in Alberta are most common in poplar-dominated forests aged 30-65 years (Westworth and Telfer 1993, Schieck and Nietfeld 1995). As stand age approaches 100 years, shrub density increases and spruce succeeds poplar through breaks in the canopy (Westworth and Telfer 1993, Lee et al. 1995). With this change in habitat structure Ovenbird numbers begin to decline (Westworth and Telfer 1993, Schieck and Nietfeld 1995). The lower numbers in old stands may be partly explained by scarcity of suitable nest sites (Appendix 3).

Rotation length, pass intervals, and the extent of upland reserves are more relevant than buffer widths to the long-term conservation of the Ovenbird and other species linked to mature poplar forests. This is particularly true for those which are most abundant in upland stands. With sufficient rotation lengths (60-70 years) and pass intervals (e.g. > 25 years), mature forest habitat can be retained on the township scale. If local extinctions can be prevented by protection of upland reserves, sustained connectivity and appropriate harvest-timing, timber management may actually favor Ovenbirds by changing the stand age-class distribution. Under the silvicultural regime depicted in Figure 1, poor Ovenbird habitat at the age-class extremes is reduced and replaced by more suitable forests of intermediate age. From this perspective, the

usefulness of the Ovenbird as an indicator species is limited; old-growth dependents may warrant greater concern.

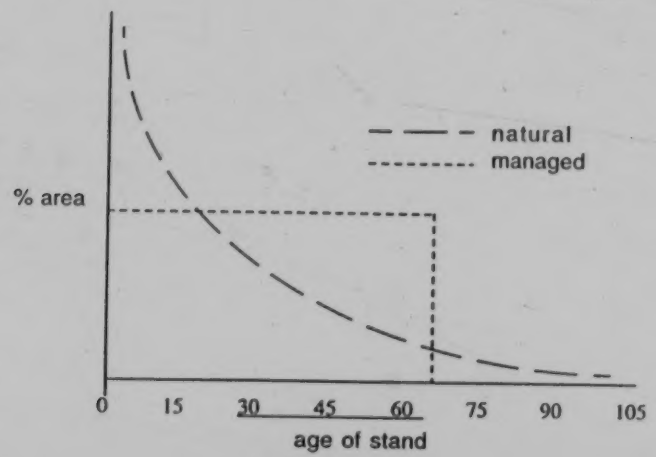


Figure 3.1. Theoretical distribution of naturally occurring stand ages and stand ages in harvested areas of an actively managed, silvicultural landscape. Underlined ages represent the reported range of greatest Ovenbird abundance.

The present study addresses the fourth possible function of buffer strips: to conserve all species breeding in the vicinity of lakes. Protection of riparian forests for water quality, erosion control, and other purposes provides the opportunity to safeguard the local bird community as well. A buffer width sufficient to contain normally breeding Ovenbirds will retain most avian species, at least until disturbance or forest maturation significantly alter forest structure and composition. My results indicate that after the first pass, 100m buffers sustain Ovenbirds for at least one year. The post-harvest absence of Ovenbirds from 20-80m buffers and data from previous research (Machtans 1996) suggest that 100m is the minimum, advisable threshold in Alberta's boreal forest. Current regulations, which require 30m buffers around small streams and small lakes (< 4ha) and 60m buffers around large, permanent rivers (Alberta-Pacific 1993), will not conserve the full complement of riparian forest-dwellers. Indeed, further evidence is required before forest managers can be confident that even 100m buffers protect the native bird community in the long term.

3.3 Research Needs

Efforts to substantiate the 100m standard should address the following, outstanding questions. They are presented in order of research feasibility, which regrettably represents the reverse order of importance.

1. Do numbers of Ovenbirds and other species that declined in Machtans' (1996) spot-map analysis (Northern Oriole, Rose-breasted Grosbeak, Philadelphia Vireo) remain stable in the majority of buffer strips over the long term?

2. Does Ovenbird pairing success remain high as post-harvest years pass?

3. Does a lakeward shift in Ovenbird territory position influence reproductive success in 100m buffer strips?

4. Does the susceptibility of 100m and 200m buffer strips to influxes of brood parasites and nest predators (Appendix 2) result in increased nest failure for forest songbirds?

5. Do answers to these questions change as townships undergo further transformation by second- and third-pass road construction and clearcutting?

Alberta's boreal mixed-wood forest has been the site of remarkable advances in riparian buffer strip research, especially in the areas of corridor use, songbird conservation, and now Ovenbird territory characteristics and pairing success. Continuing work by TROLS will make further strides by beginning to address question 1. However, no research is currently planned to investigate the more complex problems which underlie questions 2-5. Failure to follow through on these points would not only represent a missed opportunity, but might also misguide riparian forest management. Efforts to build on the growing data set, on the other hand, will enable educated integration of upland and riparian forest management, compatible with songbird conservation.

3.4 Literature Cited

Alberta Pacific Forest Industries, Inc. 1993. Timber Harvest Planning and Operating Ground Rules, Boyle, Alberta.

Burgess, C. 1997. Forested landscape patterns in the western boreal mixedwood forest of Alberta: riparian forests, fire history, canopy composition and topography. M.S. thesis. University of Alberta, Edmonton.

Emmerich, J. M., and P. A. Vohs. 1982. Comparative use of four woodland habitats by birds. Journal of Wildlife Management 46:43-49.

Lee, P.C., S. Crites, and J. B. Stelfox. 1995. Changes in forest structure and floral composition in a chronosequence of aspen-dominated mixedwood stands in Alberta. Pp. 19-61 *in* J. B. Stelfox (ed.), Relationships Between Stand Age, Stand Structure and Biodiversity in Aspen Mixedwood Forests in Alberta. Jointly published by Alberta Environmental Centre, Vegreville, AB, and Canadian Forest Service, Edmonton, AB.

Machtans, C. S. 1996. Riparian buffer strips: their value as habitat and movement corridors for songbirds in the boreal mixedwood forest of Alberta. M.S. thesis, University of Alberta, Edmonton.

Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology 10:1366-1379.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Schieck, J., and M. Nietfeld. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. Pp. 115-157 *in* J. B. Stelfox (ed.), Relationships Between Stand Age, Stand Structure and Biodiversity in Aspen Mixedwood Forests in Alberta. Jointly published by Alberta Environmental Centre, Vegreville, AB, and Canadian Forest Service, Edmonton, AB.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914-1932.

Suffling, R. H., B. Smith, and J. Dal Molin. 1982. Estimating past forest age and disturbance rates in north-western Ontario: a demographic approach. Journal of Environmental Management 14:45-56.

Westworth, D. A., and E. S. Telfer. 1993. Summer and winter bird populations associated with five age-classes of aspen forest in Alberta. Canadian Journal of Forest Research 23:1830-1836.

Appendix 1. Delineating Ovenbird Territories with Geographic Information Systems

To delineate Ovenbird territories for measurement in GRASS 4.1, I:

1. interpreted song perch clusters and counter-singing episodes to assign, where possible, each song perch to an individual male;

2. digitized song perches for each male;

3. analyzed subsets of the most thoroughly mapped birds (those with $\geq$ 85 song perches) to determine a minimum song perch threshold necessary to determine territory size;

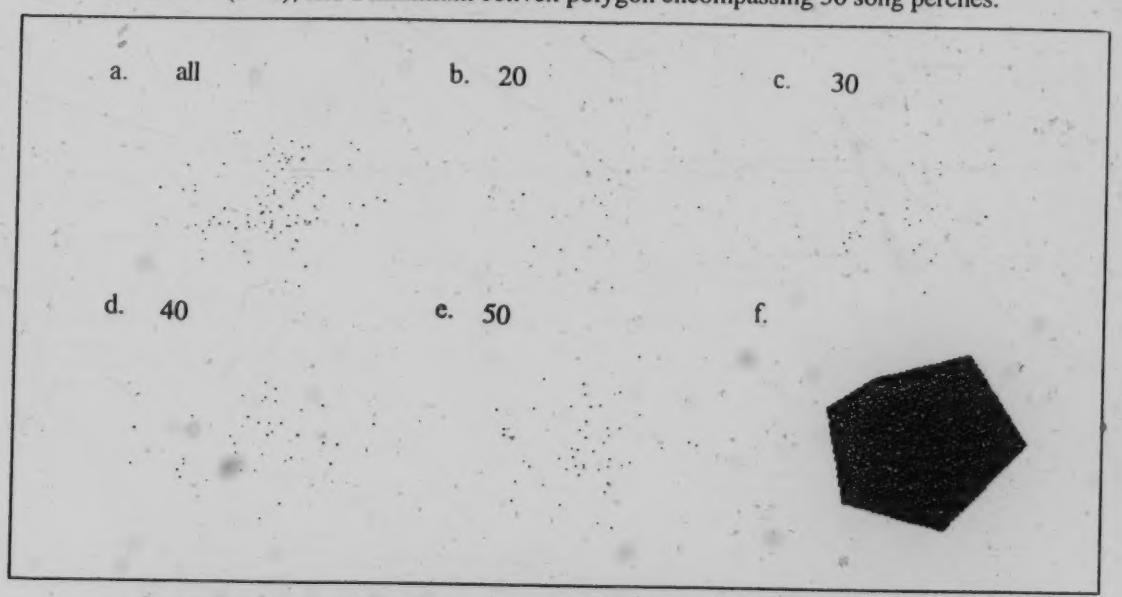
4. randomly subsampled clusters of song perches in 10-perch increments, beginning with 20 perches (i.e. 20, 30, 40 . . . see Fig. 1a-e); each cluster was replaced before a new cluster was drawn from the total number of song perches;

5. drew minimum convex polygons around each cluster;

6. graphed polygon area vs. number of song perches (Fig. 2);

7. identified the lowest number above which territories most commonly showed marginal increases in size (50).

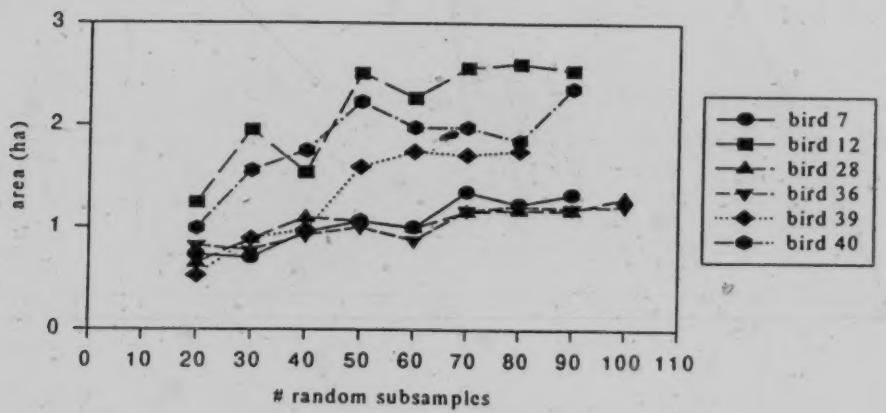
Figure 1. Delineation of the territory held by Bird 36 in 1996, with images of raster files showing: all song perches (a); 20 - 50 random subsamples in 10 song perch increments (b - e); and a minimum convex polygon encompassing 50 song perches.

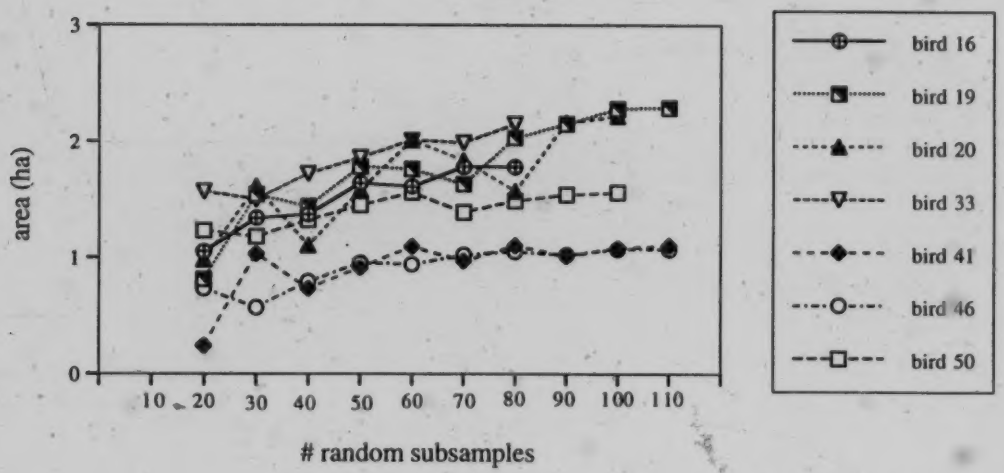


On average, 50-perch MCPs comprised 87% of the Ovenbirds' total utilized area in 1996 and 85% in 1997. Because outlying song perches artificially inflate territory size measurements, I considered 85-87% an appropriate level. Consistency between years is more important than equivalence between MCP song territories and total utilized areas. The preservation of relative sizes beyond 50 perches in both years, further justifies use of the 50-perch threshold. This approach, which uses basic GIS operations, enables efficient and reliable measurement of songbird territories from field maps. It represents an inexpensive alternative to specialized mapping software designed for x-y coordinate data.

Appendix 1. (continued)

Figure 2. The area of minimum convex polygons vs. number of random subsamples for the 6 most thoroughly mapped birds in 1996 (top), and the 7 most thoroughly mapped birds in 1997 (bottom).





Appendix 2. Nest Predators and Brood Parasites in 100m and 200m Buffer Strips

Known and suspected predators on Ovenbird nests include: eastern gray squirrels (*Sciurus carolinensis*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), weasels (*Mustela spp.*), red fox (*Vulpes vulpes*), domestic cats (*Felis domesticus*) (Van Horn and Donovan 1994), and microtine rodents (*Microtus spp.*) (Cotterill 1996). Six additional nest predators that occur in the boreal mixed-wood forest are: the Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhyncos*), the Gray Jay (*Perisoreus canadensis*), Common Raven (*Corvus corax*), red squirrel (*Tamiasciurus hudsonicus*), and Brown-headed Cowbird (*Molothrus ater*). The Cowbird also parasitizes broods by laying eggs in other species' nests for care by the host parents. Sightings of the Blue Jay and American Crow were too rare to include in data analysis. Table 1 contains pre- and post-harvest sighting frequencies for the remaining four species. One-tailed Wilcoxon signed ranks tests (WSR) were used for disturbance opportunists (Common Ravens and Brown-headed Cowbirds), whereas two-tailed WSR were applied to the forest-dependent species (Gray Jay and Red Squirrel). Non-parametric analyses were used because the preponderance of zero sightings resulted in highly skewed data. I substituted randomization testing (RT 2.0) for conventional methods according to the conditions detailed in Chapter Two, Section 3.5.

Cowbird, Raven, and red squirrel densities increased significantly after harvest in 100m buffer strips. Increases for the first two species were predicted, since they are associated with forest openings. The red squirrel's unexpected increase may have resulted from crowding of individuals displaced from the clearcut area. Cowbirds and Ravens also increased in 200m buffers. At nested control sites, predator and parasite sightings remained constant, except for an increase by Gray Jays in 1997. These results suggest that upland clearcutting promotes nest predator and brood parasite activity in both 100m and 200m buffer strips. Of the focal suite of species, red squirrels most seriously threaten Ovenbird nest survival, because their olfactory capabilities allow them to detect well-concealed Ovenbird nests. A red squirrel increase in 100m buffers, concurrent with no change in red squirrel use of 200m buffers, suggests that the former are more vulnerable to elevated nest predation than the latter during the post-harvest breeding season.

Literature Cited

Cotterill, S. E. 1996. Effect of clearcutting on artificial egg predation in boreal mixedwood forests in north-central Alberta. M.S. thesis, University of Alberta, Edmonton.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). No. 88 *in* A. Poole and F. Gill (eds.), Birds of North America. The Academy of Natural Science of Philadelphia, Philadelphia.

Appendix 2. (continued)

Table 1. Mean number of observations per hour (with SE in parentheses) of four nest predators in 100m and 200m buffers and nested controls (100m control nested in 200m control), before and after upland clearcutting. Total observation hours numbered 60.5 for 100m buffers 78 for 200m buffers and 142 for control sites before clearcutting. After harvest, sites were surveyed for 54.5h, 87.5h, and 156.5h, respectively.

Species	Treatment	n*	before harvest	after harvest	test	p
Raven	100m	36	0	0.08 (0.04)	WSR	0.03
	200m	36	0	0.07 (0.03)	WSR	0.02
	control	72	0.02 (0.01)	0.04 (0.02)	WSR	0.26
Cowbird	100m	36	0.21 (0.08)	0.45 (0.13)	WSR	0.06
	200m	36	0.09 (0.03)	0.20 (0.06)	RT	0.08
	control	72	0.28 (0.06)	0.28 (0.07)	WSR	0.59
Gray Jay	100m	36	0.65 (0.16)	1.07 (0.18)	WSR	0.43
	200m	36	0.39 (0.09)	0.23 (0.09)	RT	0.32
	control	72	0.36 (0.08)	0.19 (0.06)	WSR	0.05
Red Squirrel	100m	6	0.14 (0.05)	0.35 (0.12)	RT	0.09
	200m	6	0.30 (0.12)	0.36 (0.19)	WSR	0.60
	control	12	0.17 (0.06)	0.11 (0.05)	RT	0.48

* n represents the number of site visits for the wide-ranging, non-territorial bird species and the number of sites in each class for the territorial red squirrels. Unlike sightings of the bird species, red squirrel sightings could not be considered independent, therefore I calculated a mean squirrel sighting frequency for each site and entered this value into analyses.

Appendix 3. Ovenbird Nest Sites: Summary and Analysis of Structural Data

Ovenbird nest position has been associated with canopy gaps (Hann 1937, Ellison 1985) and deep leaf litter (Bent 1953). However, until recently, structural characteristics of Ovenbird nest sites had not been quantitatively described (Van Horn and Donovan 1994). The first thorough analysis, performed on nest sites in Ontario woodlots, confirmed litter depth as an important variable (Burke and Nol 1998). Other microhabitat characteristics that distinguished 71 nest sites from 70 random sites were: distance to edge, percent cover of bare ground, and percent cover within the seedling layer. Burke and Nol (1998) also noted moderate herbaceous and sapling cover, low shrub cover, and high canopy cover. In order to examine what variables distinguish Ovenbird nest sites in the boreal mixed-wood forest, I collected data on the 12 nests discovered during the two field seasons.

We collected data on 8 variables in the manner described in Chapter 2, Section 3.3. Instead of using rectangular vegetation plots, we used circular plots centered on the nest. Plot areas measured $100m^2$ in both sample sets. With unpaired t-tests, we compared each of the variables between the 12 sites and 36 points selected from within each of 36 Ovenbird territories. All points chosen for comparison were separated by a minimum of 100m. Where unpaired t-tests did not satisfy the conditions detailed in Chapter Two, Section 3.5, we used randomization testing (RT 2.0). So that future Ovenbird researchers in the boreal mixed-wood can benefit from our nest-searching efforts, I have included raw data describing the 12 nest sites (Table 1). Results from comparison of the two categories are presented in Table 2.

Nest sites were distinguished by significantly shorter trees and more complete canopy closure than points situated away from nests. Burke and Nol (1998) similarly reported high measures of canopy cover. Thus, the assumed relationship between canopy gaps and nest sites (Hann 1937, Ellison 1985) is refuted by both studies. Nest sites also featured fewer shrub stems, sparser shrub cover and deeper litter depths. Though these differences were not statistically significant, they too agreed with the results from Ontario. Shrub height and herb cover were virtually identical between the two categories. Considered in light of succession, these data suggest that old poplar stands characterized by tall trees, canopy gaps, and a developed shrub layer provide fewer nesting sites than mature forests, aged 30 to 80 years. This possibility supports the idea, discussed in Chapter Three, that old-growth buffer strips may not be productive habitat for Ovenbirds.

Literature Cited

Bent, A. C. 1953. Life histories of North American Wood Warblers, U. S. National Museum, Bulletin 203, Washington, D.C.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115:96-104.

Ellison, W. 1985. Ovenbird. P. 314 *in* S. B. Laughlin and D. P. Kibbe (eds.), The Atlas of Breeding Birds of Vermont. University Press of New England, Hanover, NH.

Hann, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bulletin 44:146-235.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). No. 88 *in* A. Poole and F. Gill (eds.), Birds of North America. The Academy of Natural Science of Philadelphia, PA.

Appendix 3. (continued)

Table 1. Ovenbird nest site characteristics

nest	basal area (cm^2/ $100m^2$)	canopy ht. (m)	canopy closure	shrub cover	shrub ht. (cm)	# shrub stems per $10m^2$	herb cover	litter depth (mm)
1	3665	9.0	0.95	0.05	76	20	40	90
2	2684	19.4	0.99	0.01	50	4	20	84
3	2136	10.7	0.95	0.15	86	22	40	58
4	893	17.9	0.96	0.10	84	45	20	103
5	4458	20.8	0.98	0.10	72	46	20	68
6	1683	12.9	0.99	0.13	120	27	10	96
7	2211	14.0	0.88	0.36	87	60	20	60
8	3656	19.8	0.85	0.08	85	14	60	101
9	4535	--	0.89	0.05	75	22	10	99
10	3082	20.6	0.95	0.15	93	15	30	63
11	3449	25.7	0.99	0.17	70	27	30	26
12	4227	20	0.85	0.11	91	24	35	150

Appendix 3. (continued)

Table 2. Comparison of vegetation plots situated at nest sites (n = 12) with those situated elsewhere in Ovenbird territories (n = 36). Values are reported as means with SE in parentheses.

Characteristic	Nest Site	Non-nest	Test	t	p
Basal Area ($cm^2/100m^2$)	3056 (1154)	3506 (1091)	RT		0.23
Tree Height (m)	17.35 (5.05)	20.73 (4.86)	RT		0.005
Canopy Closure	0.93 (0.02)	0.78 (0.02)	t-test	-5.50	0.0001
Shrub Cover	0.12 (0.03)	0.16 (0.02)	RT		0.29
Shrub Height (cm)	82.42 (4.81)	82.64 (4.64)	t-test	0.03	0.98
No. stems/$10m^2$	27.17 (4.54)	33.69 (3.70)	RT		0.35
Herb Cover	0.28 (0.04)	0.27 (0.02)	t-test	-0.15	0.88
Litter Depth	83.17 (9.01)	68.06 (5.67)	RT		0.21

Appendix 4. Ovenbird Nesting Data

Table 1. Ovenbird nesting data

Nest #	Site	Clutch size	Date found	Stage found	Approx. hatch date	Nest fate	Parasitized?
1	SCL200g1	5	11.6.97	incubation	22.6.97	unknown	no
2	LLB200g1	5	27.6.96	nestling	23.6.96	unknown	no
3	LLB20g4	5	17.6.97	incubation	by 26.6.97	unknown	?
4	SCL800g3	3+	27.6.97	nestling	20.6.97	unknown	no
5	SCL800g4	5	31.5.97	construction	?	unknown	no
6	SCL800g4	5	9.6.97	incubation	?	unknown	no
7	SCL100g4	5	2.6.97	construction	?	unknown	no
8	LLB800g2	?	4.6.97	laying	?	eggs depredated	?
9	SMB*	5	29.6.97	nestling	22.6.97	unknown	no
10	Louie†	5	13.6.97	incubation	24.6.97	crushed by branch	no
11	LLB800g4	5	7.6.97	laying	23.6.97	unknown	no
12	SCL200g1	2	22.6.96	nestling	20.6.96	unknown	no

* north of cutblock 05651 in TWP 70 Rge 12

† buffer strip on the south border of the southern portion of cutblock 28871 in TWP 71 Rge 12

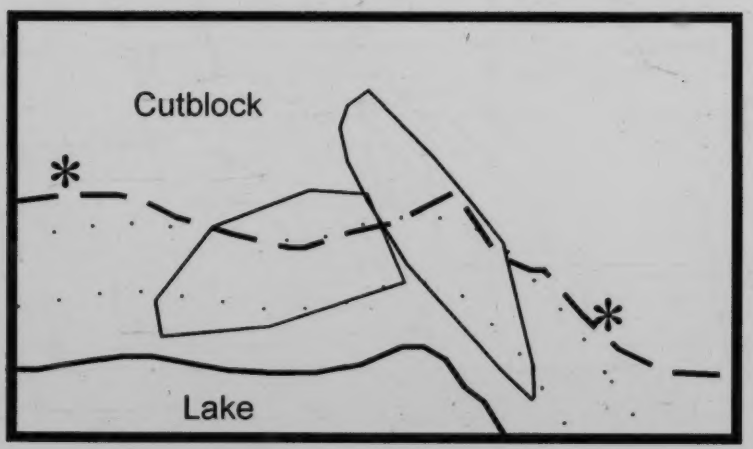
Appendix 5. Ovenbird Territories Before Harvest (1996) and After Harvest (1997)

— — Cutblock boundary · · · · · 50m zone

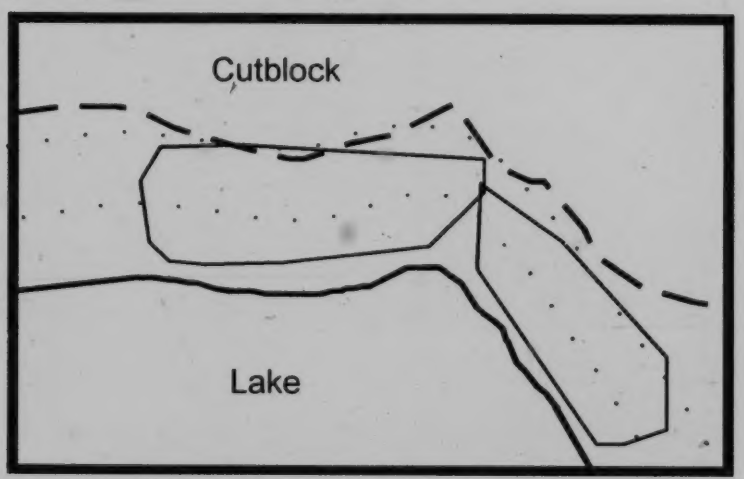
——— Riparian forest edge ⬭ Ovenbird territory

✱ Approximate position of Ovenbird territory with <50 mapped perches

LLB 100 grid 1 pre-harvest

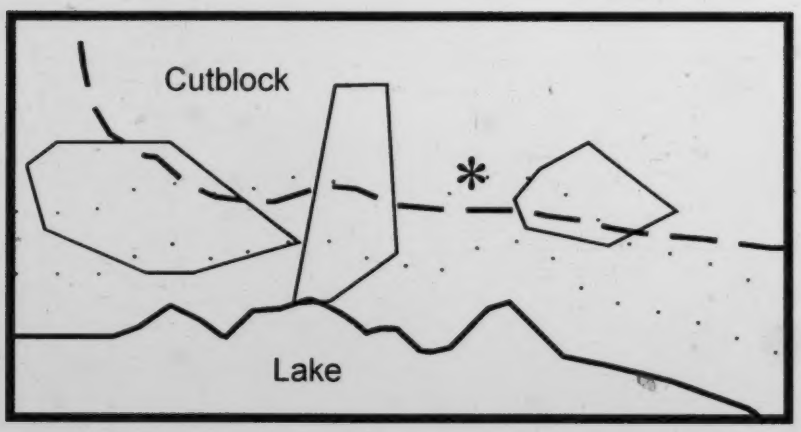


LLB 100 grid 1 post-harvest

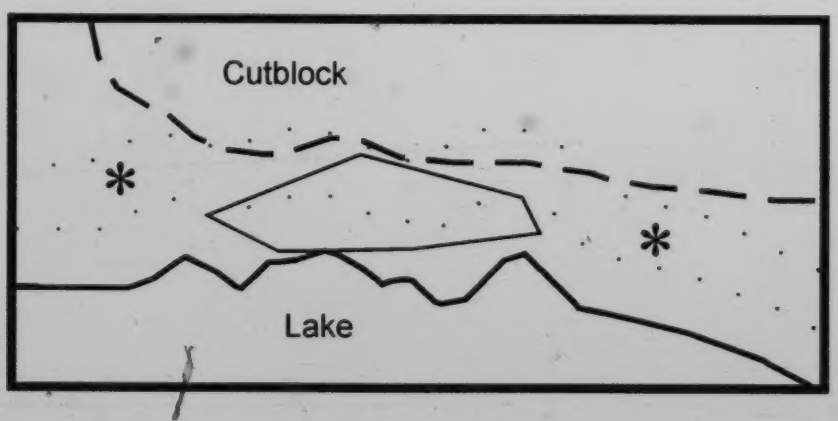


Appendix 5. (Cont.)

LLB 100 grid 2 pre-harvest

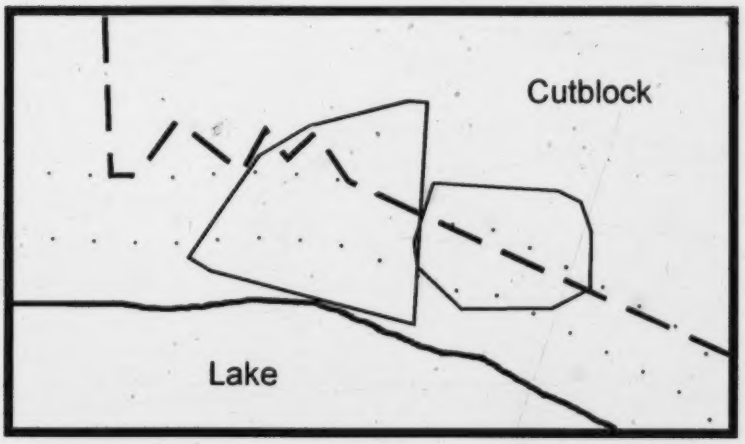


LLB 100 grid 2 post-harvest

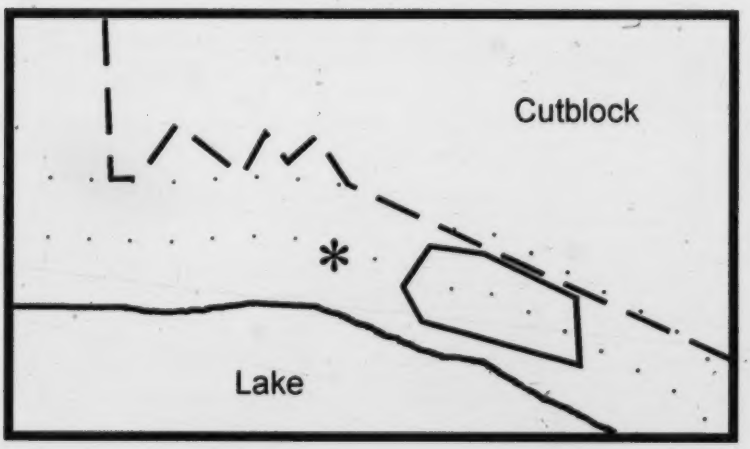


Appendix 5. (Cont.)

SCL 100 grid 4 pre-harvest

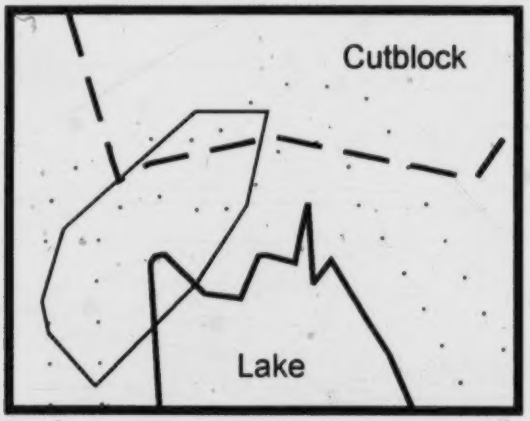


SCL 100 grid 4 post-harvest

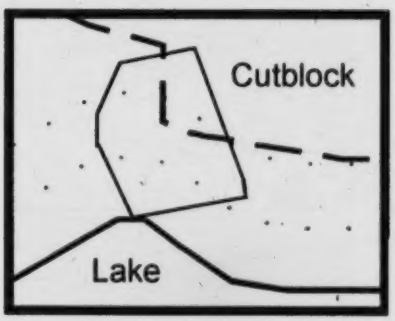


Appendix 5. (Cont.)

SCL 100 grid 5 pre-harvest

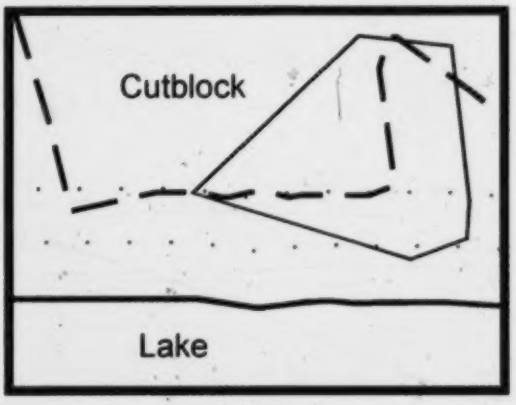


LLB 100 Dewey post-harvest

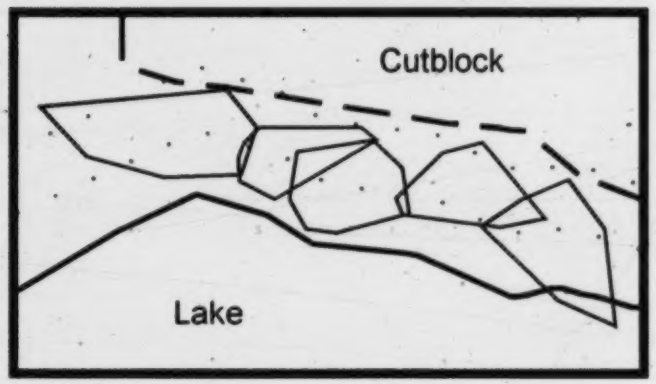


Appendix 5. (Cont.)

LLB 100 Louie post-harvest

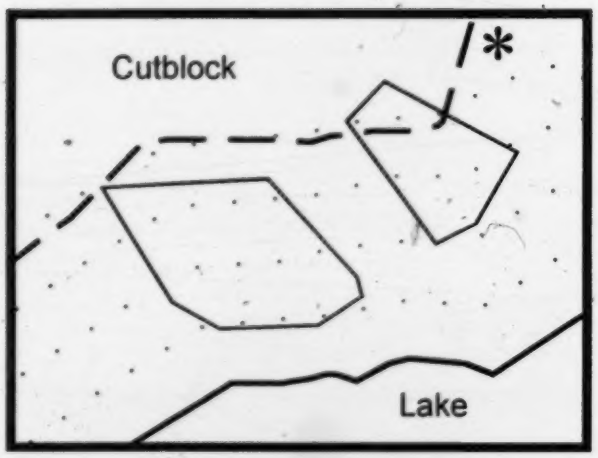


LLB 100 Basecamp post-harvest

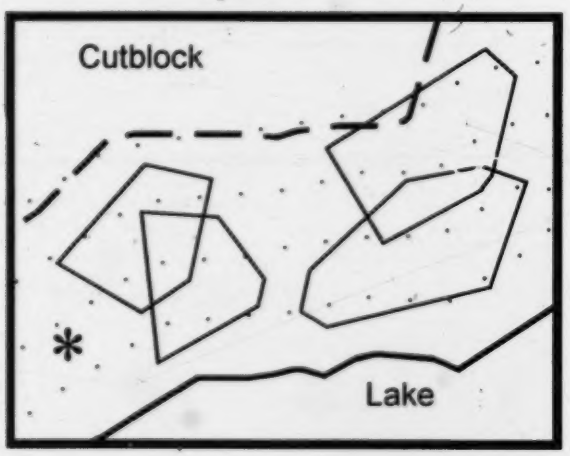


Appendix 5. (Cont.)

LLB 200 grid 1 pre-harvest

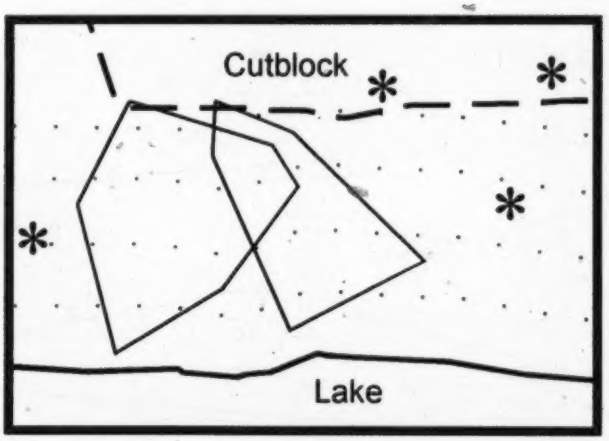


LLB 200 grid 1 post-harvest

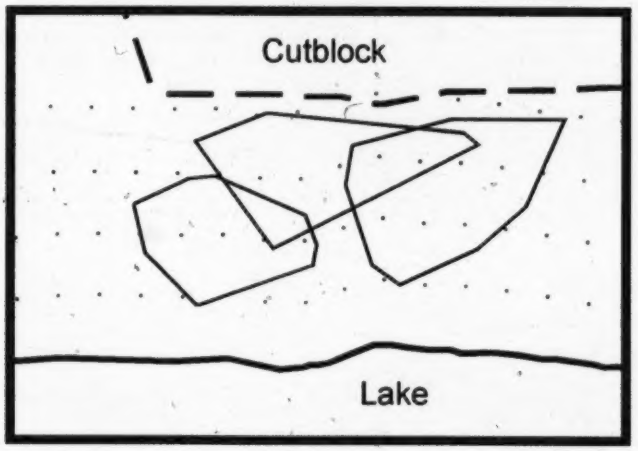


Appendix 5. (Cont.)

LLB 200 grid 2 pre-harvest

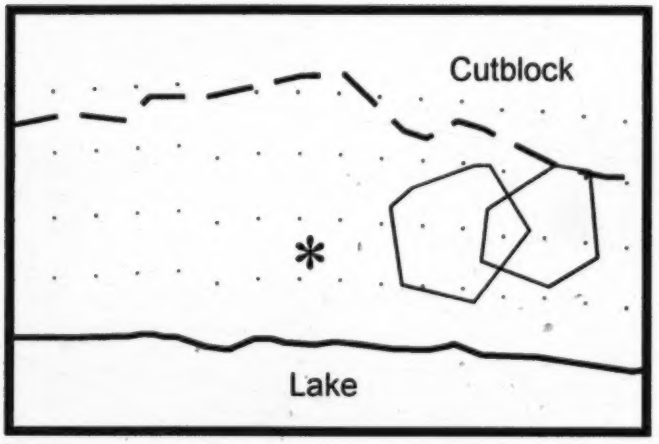


LLB 200 grid 2 post-harvest

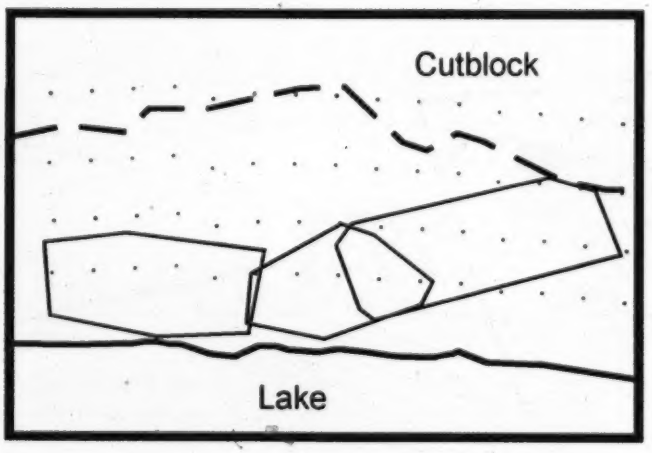


Appendix 5. (Cont.)

SCL 200 grid 1 pre-harvest

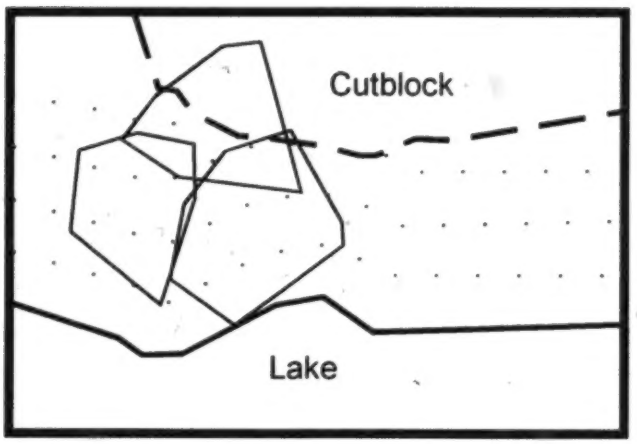


SCL 200 grid 1 post-harvest

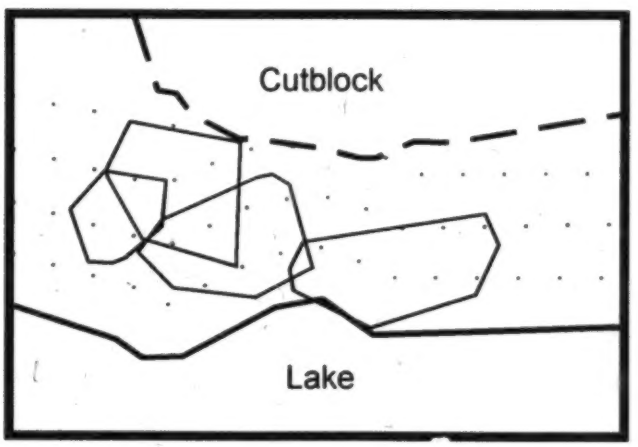


Appendix 5. (Cont.)

SCL 200 grid 2 pre-harvest

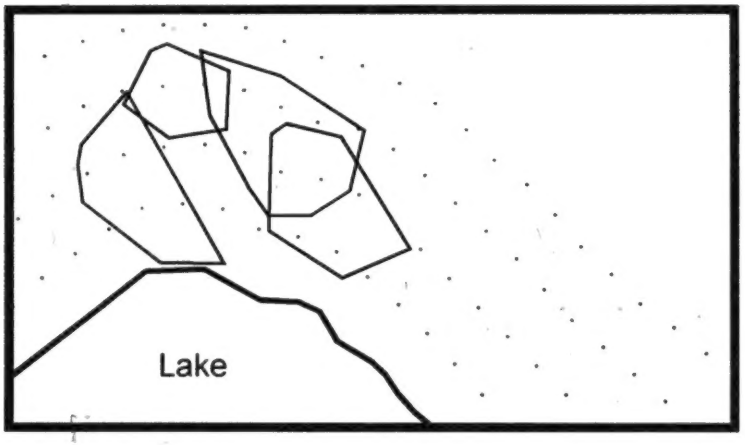


SCL 200 grid 2 post-harvest

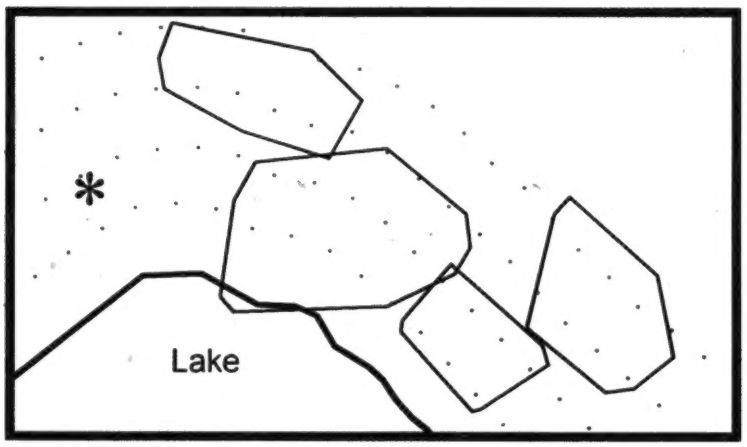


Appendix 5. (Cont.)

LLB 800 grid 2 pre-harvest

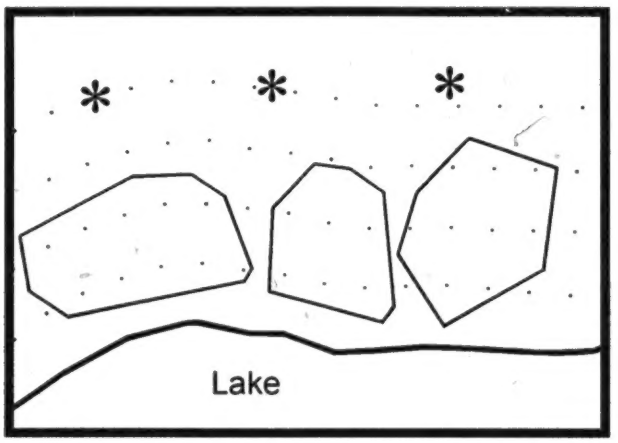


LLB 800 grid 2 post-harvest

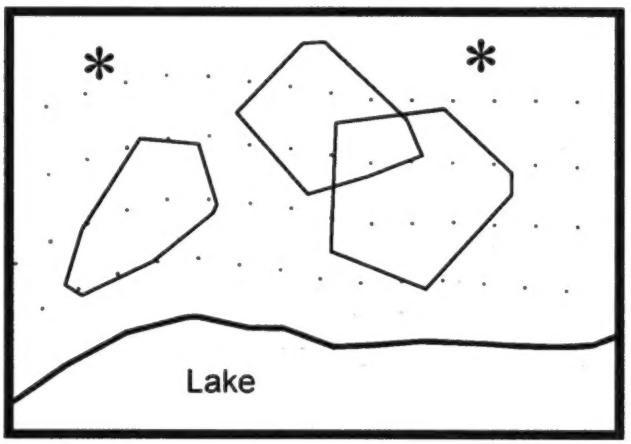


Appendix 5. (Cont.)

LLB 800 grid 3 pre-harvest

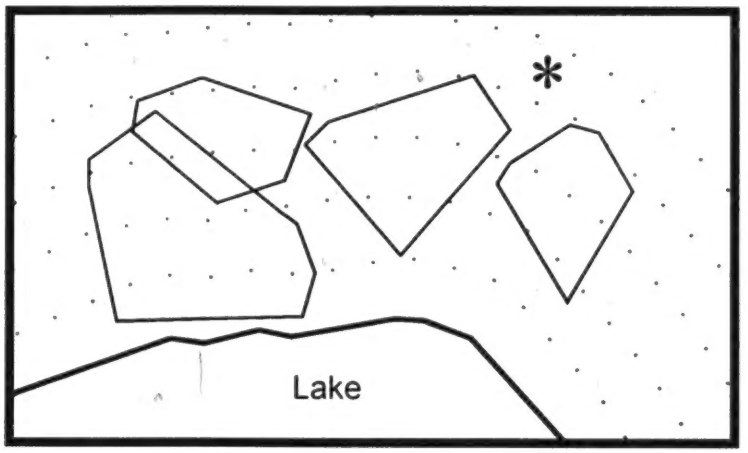


LLB 800 grid 3 post-harvest

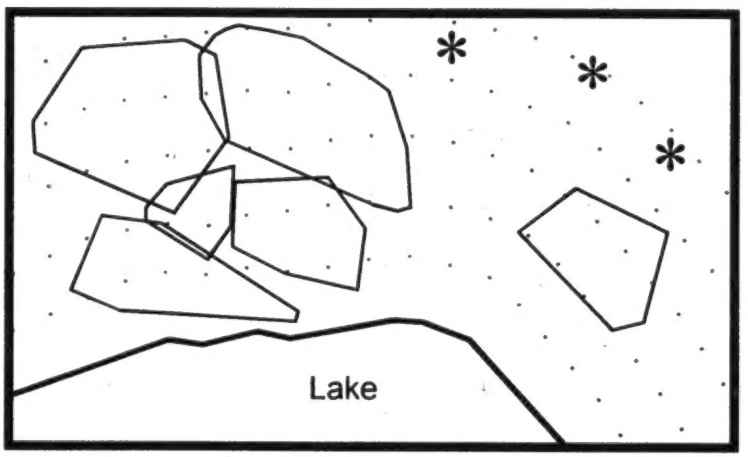


Appendix 5. (Cont)

LLB 800 grid 4 pre-harvest

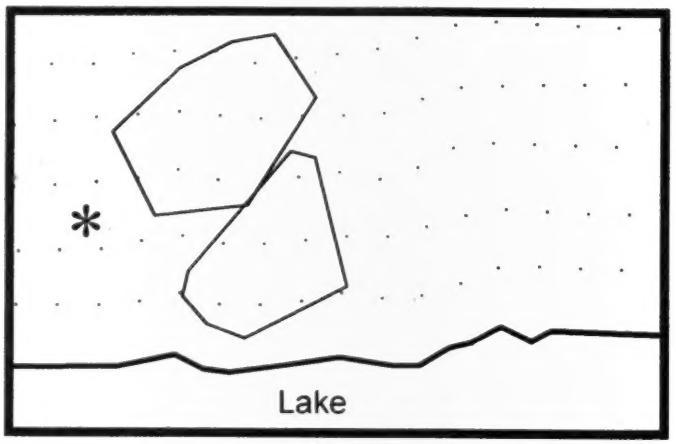


LLB 800 grid 4 post-harvest

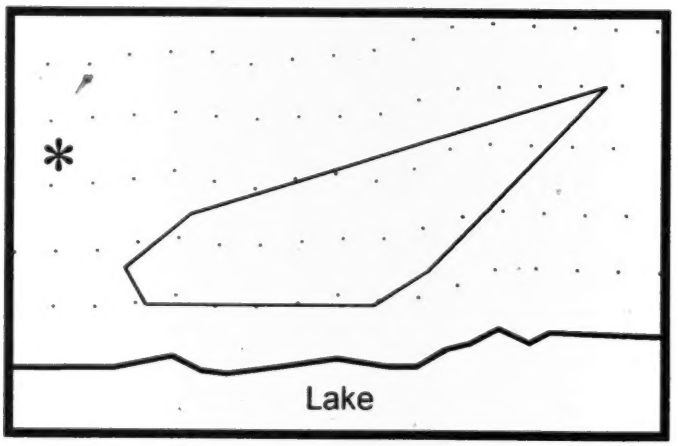


Appendix 5. (Cont.)

SCL 800 grid 1 pre-harvest

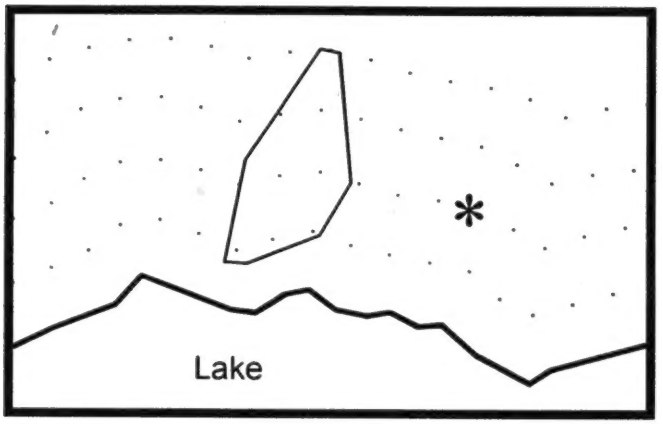


SCL 800 grid 1 post-harvest

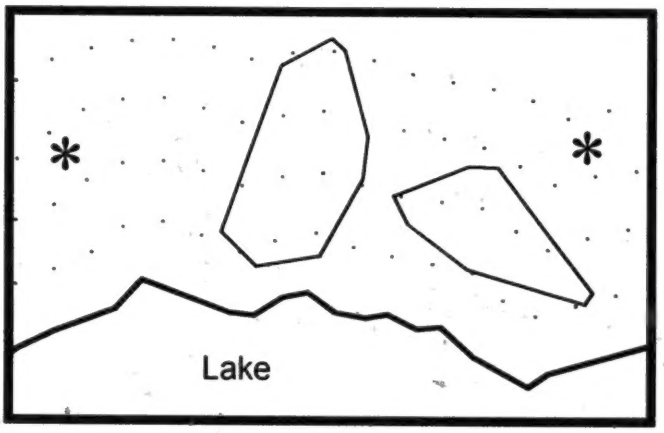


Appendix 5. (Cont.)

SCL 800 grid 3 pre-harvest

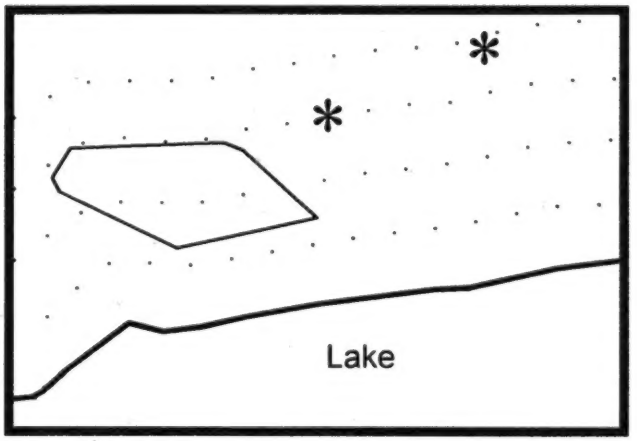


SCL 800 grid 3 post-harvest



Appendix 5. (Cont.)

SCL 800 grid 4 post-harvest



Appendix 6. Distribution of Tennessee Warblers in Interior, Clearcut, and Riparian Sites

Derived with the same methods used for Figures 3 and 4 of Chapter Two, the following graphs show Tennessee Warbler (TEWA) concentration at the riparian forest edge. The pattern is opposite that observed for Ovenbirds. However, as with Ovenbirds, Tennessee Warbler abundance was similar between clearcut edges and forest interiors. Because TEWA territories are small enough to fit in 50m zones, the song perch data do not show the boundary effect observed for Ovenbirds.

If the understory at a clearcut edge develops to resemble the vegetation structure of a riparian forest edge, densities of the shrub-foraging TEWA may increase. Research designed to test this hypothesis would clarify the degree to which edge and lake adjacency explain TEWA concentration at the riparian ecotone.

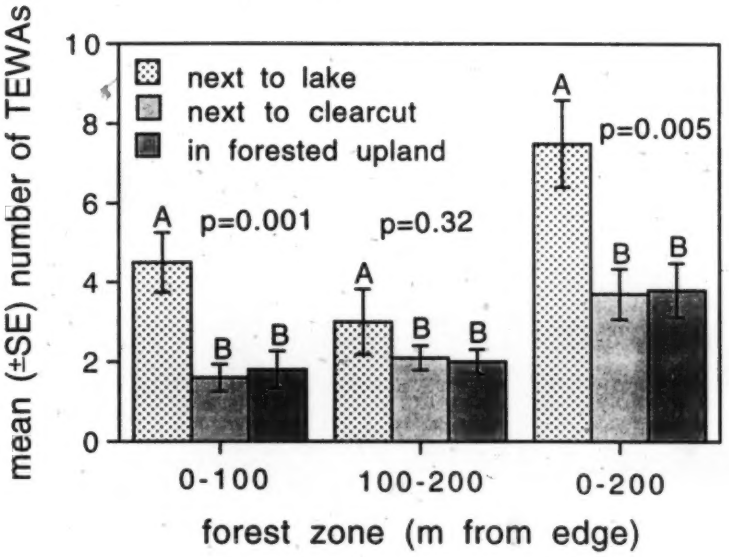


Figure 1. Mean number of Tennessee Warbler territories in forests next to lakes (n=6), forests next to clearcuts (n=10), and in continuous upland forest tracts (n=10). Differences determined by one-way ANOVA. Column letters denote homogeneous groups identified by Tukey's-b post hoc test.

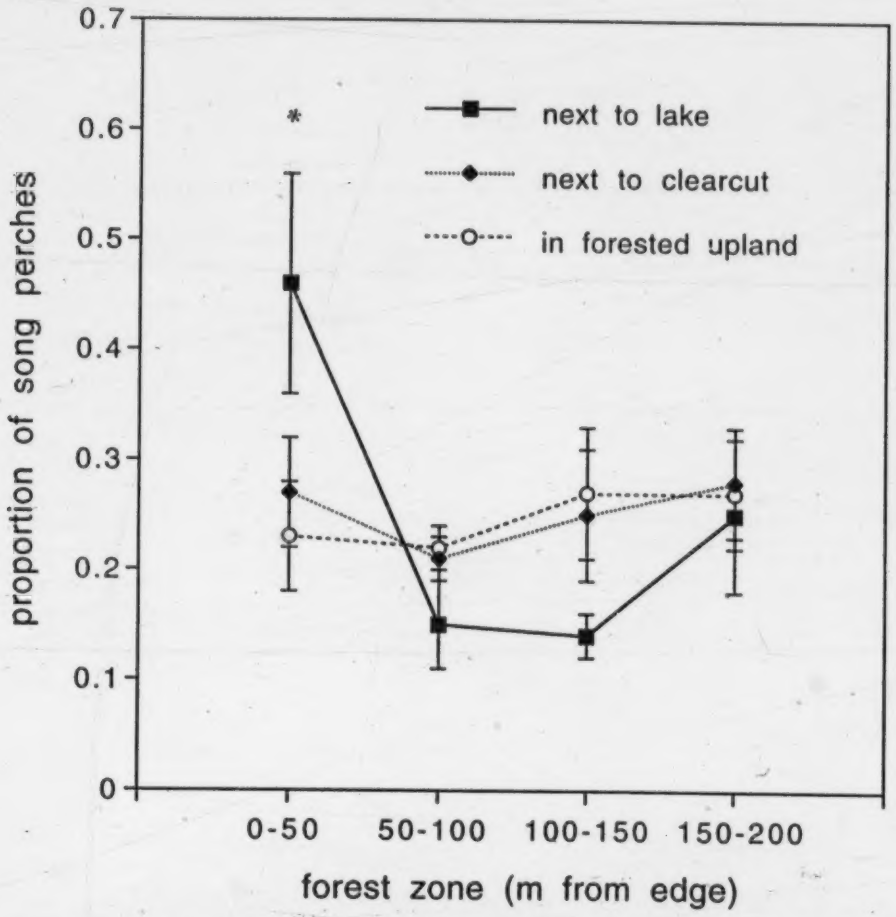


Figure 2. Mean proportion of Tennessee Warbler song perches (± SE) in four designated zones at six sites next to lakes, eight sites next to clearcuts, and eight sites in forested uplands. * represents significant difference ($p<0.1$) as determined by one-way ANOVA.